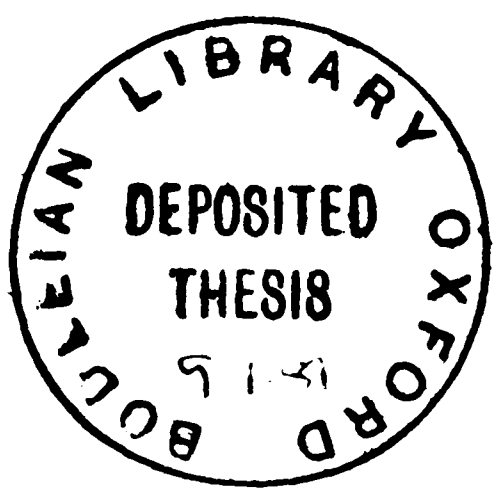
INTERSPECIFIC COMPETITION BETWEEN BLUE AND GREAT TITS

by

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Interspecific competition between blue and great tits.

ABSTRACT

Great tits (Aves:Passeriformes; Parus major) and blue tits (Parus caeruleus) nested in boxes in Wytham Woods near Oxford. The breeding densities of both species were limited by the availability of nest sites. The larger great tits were dominant in obtaining nest boxes. This was most important where breeding sites were scarce. The two species did not maintain interspecific territories or interfere with interspecific nest site spacing beyond the immediate vicinity of the nest. Blue and great tit numbers fluctuated in parallel where nest sites were not limiting resources. Annual changes in breeding numbers of great tits were negatively related to blue tit breeding density but great tit density did not seem to affect changes in the blue tit population.

Overlap in the feeding sites of blue and great tits was greatest during the summer and interference competition was lowest at this time. The nestling diets of the two species were very similar. Despite an apparent abundance of food for nestlings, adults were pressed to feed large broods. Food for nestlings was probably a limiting and depletable resource.

The date of clutch initiation of great tits, but not blue tits, was retarded at high densities of blue or great tits. The clutch sizes of both species were probably negatively affected by high breeding densities of congeners but the results were not clear cut.

Heavy great tit fledglings are most likely to survive to breed. Great tit fledglings were heavier at low densities of blue tits. An experiment in which blue tit young were removed from a section of the Woods, showed that great tit nestlings were heavier and developed faster, and that female condition was better, than in a control section or section where blue tit broods were supplemented.

In terms of resource competition, blue tits were the better scramble competitors and great tits the better interference competitors.

In memory of

SARAH

who grew while this thesis was being written.

We grieved that she could not know the

less capricious side of Nature but

cherish the few hours

we had with her.

ACKNOWLEDGEMENTS

During my first few weeks in Oxford, Chris Perrins, my supervisor, outlined many of the problems discussed in this thesis. Chris stood by patiently when I announced that the ideal species for studying interspecific competition would be skylarks and meadow pipits and the ideal place would be Skomer Island. The days spent finding pipit and lark nests convinced me of the wisdom of studying birds that nest in boxes. Nevertheless, my two field seasons on Skomer provided time to think about competition. For this time I am grateful to the Nature Conservancy, the West Wales Naturalists' Trust and to the warden of Skomer and his wife, Mike and Roseanne Alexander.

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My wife, Midge, typed the final copy of the thesis and always knew that I meant 'positive' when I said 'negative'. For her forbearance, understanding and insightful criticism I am particularly grateful.

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CHAPTER 1

Introduction

Great tits (Parus major) have proved an excellent species for studying the breeding dynamics of a vertebrate population in a nearly natural environment as well as for studying a number of other diverse problems. Lack (1966) listed several of their virtues. Two important features are that they prefer nest boxes to natural breeding sites and they winter where they breed. Much was learned from an early study in Holland presented in a landmark paper by Kluijver (1951) and another Dutch study on feeding by Tinbergen (1949). The success of this work prompted David Lack to initiate a long term study of tits in Wytham Woods, near Oxford, in 1947.

The great strength of the Wytham study is the long, continuous record of what has happened in the Woods. Data on all species using the nest boxes have been kept since the beginning. Besides the great tit, the blue tit (Parus caeruleus) has been the other major species nesting in boxes in Wytham Woods. With over 30 years of breeding and population data it seemed that a study of both species, particularly for evidence of interspecific competition, might prove very interesting.

A good general review of blue and great tits is in Perrins (1979). Lack (1966) summarizes many of the details of the Wytham tit study.

There is now a considerable body of theory about interspecific competition which is only just coming under the critical scrutiny of quantitative field data and ex-

periments under field conditions (e.g. Connell 1975, Dhondt 1977, Adams 1980, Högstedt 1980). Data from the populations of blue and great tits could be used to examine two species that almost certainly compete for a range of limiting resources, most notably food and breeding sites (nest boxes).

THEORETICAL BACKGROUND

In each chapter of this thesis I will provide an introduction to the problems discussed within that chapter. Here, however, I will outline some concepts which provide an overview of competition and a common thread for the chapters that follow. This is in no way intended to be a comprehensive review, rather a précis of relevant ideas.

Density dependence and population regulation

Animal populations, primarily vertebrate populations, are observed to remain relatively stable over long periods of time. This ability to persist has lead to the not unreasonable conclusion that there might be some sort of homeostatic mechanism leading to the regulation of populations. The logistic or sigmoid equation ($dN/dt = rN-rN^2K^{-1}$; where N is the population size, r the intrinsic rate of increase, and K the carrying capacity or population size at saturation) is the deterministic outgrowth of the homeostatic concept (Maynard Smith 1974). The equation also works rather well for describing the growth of cell cultures of yeasts and Paramecium (Gause 1934).

Problems arise in moving from descriptive, deterministic models to causal, stochastic models. The essence of

the problem is this; the existence of populations of species means that they have persisted for rather a long time. Thus, persistence follows from existence. In any dynamic model with some degree of environmental uncertainty, persistence requires regulation, i.e., negative feedback. Thus, regulation and persistence are given a priori. This means that statistical tests for density-dependent regulation of natural populations will tend to be tautological (but not experimental tests). More elegant treatment of this problem may be found in Reddingius (1971), Orians (1974) and Royama (1977). The problem is more than just a clever bit of metaphysics, it means that most simple tests for the density-dependent regulation of populations are bound to succeed, given enough data. For example, given the simple model $N_{t+1} = R_t N_t$ (where N is the population size at time t and R_t is the multiplication function for the change in population size from t to t+1), R and N are bound to be negatively correlated whether or not R is causally dependent on N.

The multiplication factor, R, may be affected by almost anything. In addition to intraspecific density, it may be affected by the density of other species and by environmental factors such as weather or food supply. Some of these other factors may in turn be density dependent, e.g., the effect of a food shortage on R_t may be greater at a high than at a low N_t. In fact, if there is a causal relationship between R and N then presumably it operates through limiting resources such as food or breeding sites by either regulating the birth rate, death rate or migration

of a population. In this thesis I shall be interested in whether there is not only an effect of intraspecific density on components of R, but an interspecific effect as well. There is no a priori reason why certain components of R should be more dependent on interspecific density than on intraspecific density. Ultimately, however, by extension of the Gause or Lotka-Volterra equations, R should be more dependent on N than on the density of some other species (N'), at least at low densities of N_t. Slade (1977) and Poole (1978) discuss some practical aspects of predictive population models.

In Chapter 2 I use a modified key-factor analysis to examine some factors that may affect R for both blue and great tits. Of primary importance will be the effect of interspecific density on R. In Chapters 6 and 7 I examine more closely the effect of inter- and intraspecific densities on the breeding success of blue and great tits, especially clutch size and the weight of nestlings at fledging. In Chapter 5 I investigate the effect of breeding densities on natal dispersal and the timing of breeding, which may be related to reproductive success and survival.

Competition

If the presence of individual A decreases the fitness of a second individual B, then A may be defined as a competitor for B. In most instances there will probably be some reciprocity so that A and B may be called competitors or be in competition with each other. The most likely cause of competition is a limiting resource used by both A and B. Resource competition may be of two types, scramble (=exploi-

tation) competition or interference (=contest) competition. Scramble competition occurs when competitors both utilize a common resource and decrease the availability of the resource simply by using it. For example, A might remove seeds from a common feeding site and thus reduce the availability of seeds for B. Interference competition occurs when an individual attempts to limit the access of others to a resource, e.g., by defending a territory.

The same concepts and terminology may be extended to groups of individuals so that we may speak of interspecific competition. While behavioural responses to competition must be seen as operating at the level of the individual, there are no major pitfalls to describing all competition between individuals of one species and another with collective terms, e.g., interspecific interference competition.

In Chapters 2 and 3 I will examine competition for space, both breeding territories and nest boxes. The direct observation of competition is difficult and here it is mostly inferred from population data (Chapter 2) and the history of nest-box use (Chapter 3). In Chapter 4 I will investigate competition for food and the change in the level of competition with season. Competition for space is interference competition almost by definition because space cannot be depleted, while competition for food may involve elements of both interference and scramble competition.

Lotka-Volterra models

The two species extension of the logistic equation is the Lotka-Volterra or Gause equation $dN/dt = rN - rN^2K^{-1} - r\alpha NN'K^{-1}$ (Volterra 1926, Lotka 1932, Gause 1934). The

additional term $r\alpha NN'K^{-1}$ describes the effect of the population density N' of a competing species on the population change dN/dt. The term α is called the competition coefficient and is a measure of the effect of the numbers of a competing species on the intrinsic rate of increase, r.

By inference, the competition coefficient is also a measure of similarity between two species. As it approaches 1.0 the effect of interspecific density approaches the effect of intraspecific density and conditions for the stable coexistence of the two species become tenuous. This is the essence of the competitive exclusion principle (Gause 1934). The principle is reviewed and reformulated by Armstrong and McGehee (1980).

Further terms for interspecific competition may be added, each with an associated competition coefficient. This multi-species model has given rise to the concept of diffuse competition (MacArthur 1972). This is more in recognition of the strong effect that many minor competitors could have on r than a definition of a particular mode of competition.

The Lotka-Volterra model has many drawbacks. Amongst them is the assumption that the competition coefficient is constant over all densities (Ayala et al 1973). Also, in the multi-species models the interaction of competition coefficients may not be additive (Wilbur 1972). Wangersky (1978) reviews Lotka-Volterra population models.

Niche theory

Most ecologists have a working definition of niche but formal definitions vary widely. Many currently used definitions include a measure of fitness or reproductive success which is more applicable to theoretical use (e.g., Hutchinson 1957; Pielou 1976). Levins (1979), although dissatisfied with the term 'niche', showed that environmental variance affected coexistence conditions and thus would form higher order resource dimensions. For certain purposes the term has been given very restricted meanings, e.g., Cohen (1978) uses 'niche' to refer only to 'trophic dimensions'. I shall use it in the sense of Pianka (1976) to refer to the resource utilization spectra of species.

There are two important concepts in multi-species systems, niche width and niche overlap. Niche width is a measure of the diversity of resources utilized by a species or individual. For a single resource dimension this might be measured by the Shannon information index (Shannon and Weaver 1949) which would weight each unit of the resource dimension according to the frequency with which it was used. Pielou (1972) discusses the measurement of niche width further. Optimal foraging theory predicts that as competition within a resource dimension increases, the niche width should increase as more marginal elements of the dimension are utilized (MacArther 1972, May 1974, Charnov 1976). However, in patchy environments niche width may decrease as competition forces a species to use only a limited number of patches (Cody 1974, Werner 1976). Interspecific comparisons of diversity may indicate the relative

extent to which species are specialist or generalist. However, only changes in diversity should be used to infer the effects of competition.

Niche overlap is a measure of the extent to which two species (or other organismic units) use the same resources. The measure of overlap may be compressed into a single index that indicates the extent to which all resources or a subset of resource dimensions are used in common by two species. The overlap index is not directly comparable with the competition coefficients of the Gause or Lotka-Volterra equations despite the general use of 'α' to denote both. There are two major conceptual differences. First, many overlap indices are symmetric or non-directional, i.e., the overlap of species A with species B equals the overlap of B with A. Various overlap indices are discussed by Horn (1966), Levins (1968), Pianka (1973), Schoener (1974) and May (1975). Competition coefficients are not constrained to be symmetric. Second, competition coefficients are based on population sizes which are related to the mean fitness of individuals in each species. Overlap indices, as defined here, are based on resource use. However, attempts have been made to assess the fitness component of resource overlap, e.g., Vandermeer (1969). Overlap in the use of resources that are not limiting will not affect fitness. Nevertheless, a recent comparison of the niche overlap and competition coefficients of two avian populations showed that the values were similar (Högstedt 1980).

Niche width and overlap are discussed in Chapters 3 and 4 in relation to the use of space and food. In the

other chapters, niche width and overlap are not discussed explicitly but the concepts underlie many of the discussions of competition.

Why do birds come in different sizes?

If two sympatric congeners are of different sizes there are two ways to go about explaining the difference and the two explanations are by no means exclusive of one another. The first explanation stems directly from the competitive exclusion principle, i.e., two sympatric species cannot have the same niche. One species will be large and exploit resources requiring a large body size, e.g., large seeds. The other species will be small and use a different resource spectrum, e.g., smaller seeds. The Galapagos finches have probably made more than their share of contributions to this type of explanation (Lack 1947, 1969; Hamilton and Rubenoff 1967; Grant et al 1976; Abbott et al 1977).

The second explanation ultimately depends on the competitive exclusion principle, but it was derived via a more complex route. In the logistic equation the terms r and K may be viewed as taking on different importance depending on N. When N is low r is more important than K in determining the rate of population increase. However, as N approaches K, dN/dt approaches zero regardless of r. This has lead to the heuristically valuable concepts of r- and K-selected species (MacArthur and Wilson 1967, Southwood 1976). The r-selected species are those that tend to be in environments where $N \ll K$, so that a high fecundity is important. The K-selected species tend to occur in stable envir-

onments where N ≐ K, so that resource accrual becomes very important. The r-selected species will tend to be good scramble competitors because resource defense is counter-productive in an environment that has abundant resources. K-selected species will tend to be good interference competitors because they live in environments where resources are limiting. A good interference competitor will rely on large body size to win contests for resources while the scramble competitor should be the optimum size for most efficiently exploiting the available resources. In the case of two sympatric congeners using similar resources, the interference competitor will be larger than the scramble competitor. Coexistence of the two species can occur because of a spatially or temporally patchy environment. Interference competitors will require richer, defendable patches of resources, while scramble competitors will be able to exploit sparse resources economically. Interference and scramble competition,or r- and K-selected species, both imply extreme polarity but it should be remembered that a continuum connects the two poles.

On a relative scale the smaller blue tits tend to have more of the traits of an r-selected species and the great tits, about twice the size of blue tits, appear to have more of the attributes of a K-selected species. In general, the great tits appear to be the better interference competitors and the blue tits the better scramble competitors. During the breeding season blue and great tits are in direct competition for similar food items and nest sites and the scramble versus interference competition features of body

size may be most important. However, the two species are more segregated during the winter when the relationship between body size and resource utilization may be more important.

CHAPTER 2

Breeding Populations

If blue tits and great tits are in competition with one another then a logical place to begin looking for evidence is with the annual censuses of breeding numbers. Competitive interactions between the species should result in some type of negative relationship between the numbers of the two species. However, various environmental constraints may mask such negative relationships. If so, density independent factors such as food supply, weather or availability of breeding sites will have to be considered in any analysis of breeding numbers in order to account for their contribution to changes in breeding numbers.

In this chapter I examine two general ways in which the numbers of one species might be negatively related to the numbers of a second. First, competition for a resource may vary according to the scarcity of the resource. The scarcity of the resource may be absolute or relative to the number of one or both species. If, as a resource becomes scarce, one species does relatively better than the other, then competition between the species may be inferred. It may be assumed that which ever species did relatively better during the shortage was the better competitor for that resource.

Second, changes in the number of one species may be negatively related to the numbers of a second species. This is essentially the Gause (1934) model of interspecific

competition. That is, the equilibrium density for one species depends, in part, on the number of competitors of a second species. The possibility of this type of relationship between blue and great tits will be examined with a type of modified key-factor analysis. The models analyse both breeding numbers and environmental factors such as weather and food.

STUDY AREA AND METHODS

From 1947 until 1958 Marley Wood was used as the main study area in Wytham Great Woods (Wytham). There have been about 100 nest boxes in Marley Wood since 1947 and about 200 since 1950. Beginning in 1958 nest boxes were put up in other parts of Wytham so that by 1963 there were boxes in eight recognized sections of the wood as shown in Figure 2.1. The number and positions of boxes have remained about the same in all areas since 1964. A ninth area, Pasticks, was added in 1977. Between sections there are some habitat differences. However, in general, the whole of Wytham is oak-mixed woodland. One notable difference between sections of the Wood is the density at which nest boxes are provided (Table 2.1).

Since 1964 the only major change to the study area was the replacement of wooden nest boxes with concrete boxes between 1973 and 1978. The most noticeable effect of the change in box type was a reduction in the predation of nestlings (Dunn 1977). However, since about 1974 the sparrowhawk population has increased so that the predation of adults and the predation of young during the post-fledging period has probably increased (Geer 1979).

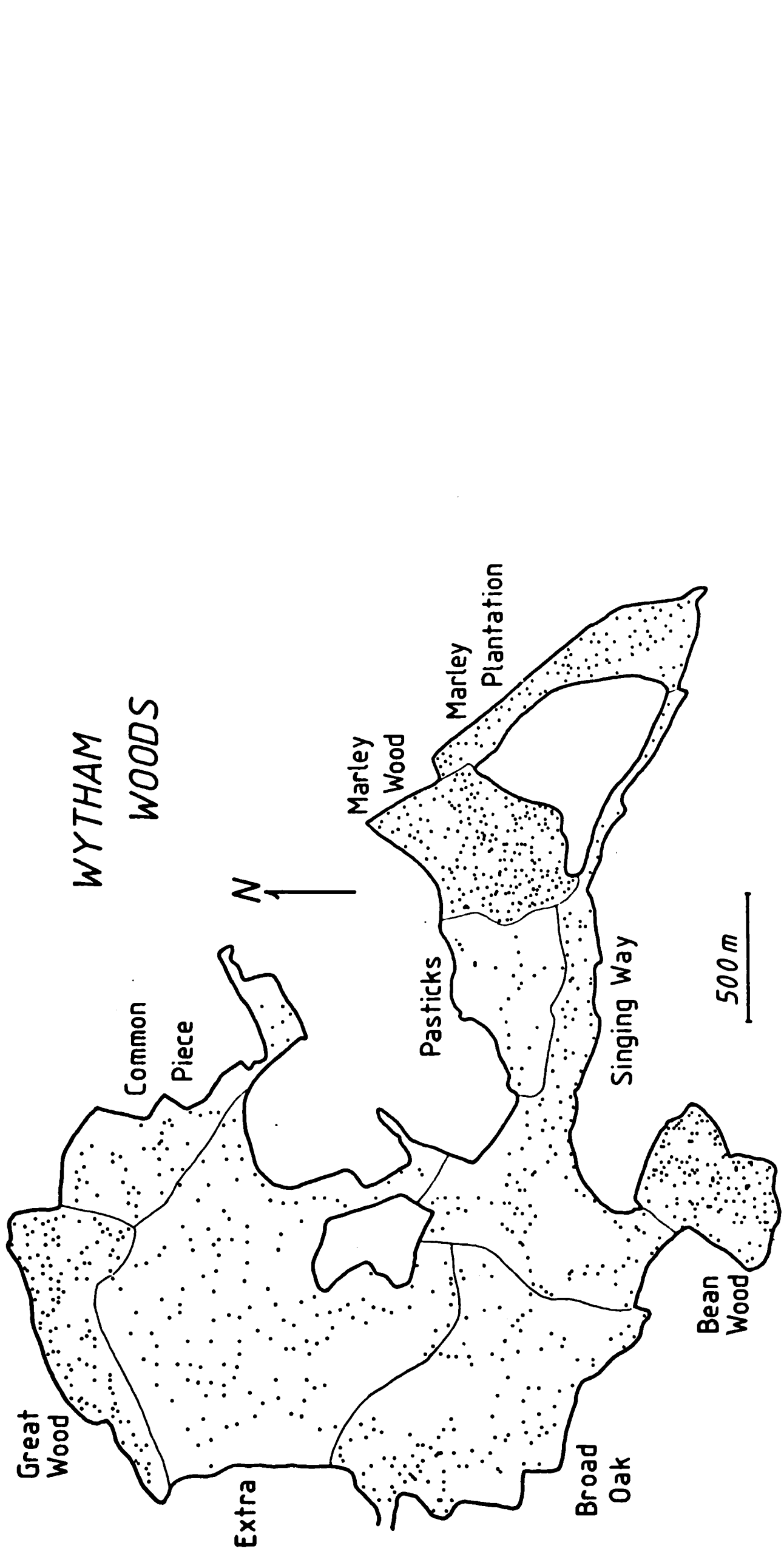


Figure 2.1 Map of Wytham Woods showing the positions of nest boxes in the nine sections of the Wood. Pasticks was added in 1977.

Table 2.1 Area, number of boxes and nest-box density in different sections of Wytham Woods.

SECTION	AREA(ha)	NUMBER OF BOXES	BOX DENSITY (Pairs ha^{-1})
Marley Wood (B)	26.7	214	8.0
Great Wood (W)	25.9	107	4.1
Broad Oak (O)	35.6	115	3.2
Extra (E)	60.7	122	2.0
Common Piece (CP)	19.0	45	2.4
Bean Wood (C)	17.0	134	7.9
Marley Plantation (MP)	18.6	88	4.7
Singing Way (SW)	27.1	134	4.9
Pasticks (P)	20.4	24	1.2

During the period when wooden boxes were replaced by concrete boxes there was an increase in the number of blue tits found breeding in boxes. The change to concrete boxes could have caused the increase or the increase could have been coincidental. In the early years of the study Gibb (1954) found that up to one-third of the blue tits in Marley Wood might be using natural sites as opposed to wooden boxes. In the following chapter I show that at least in sections of the Wood with a high density of boxes, most (90%) blue tits used nest boxes in a year of high breeding density. Factors other than the change of box type may be responsible for the difference between my findings and those of Gibb. Gibb's estimate was based on the percentage of unringed nestlings trapped during the early postfledging period whereas I used the percentage of territories in which the pair used a nest box to rear their young.

In my analysis of population data I shall assume that the construction of nest boxes has had no effect on the number of blue tits using boxes. It is best to briefly support this assumption now. First, the trend toward more blue tits is not local. It has occurred over much of Europe since the 1940's or 1950's. Figure 2.2 shows this trend in the ratio of blue tit to great tit pulli ringed in the U.K. By comparison, the ratio of blue tits to great tits breeding in boxes in Marley Wood showed a similar trend though the relative increase in blue tits was very dramatic from 1972-1974. Secondly, there is no indication that blue tits actually prefer the concrete boxes when

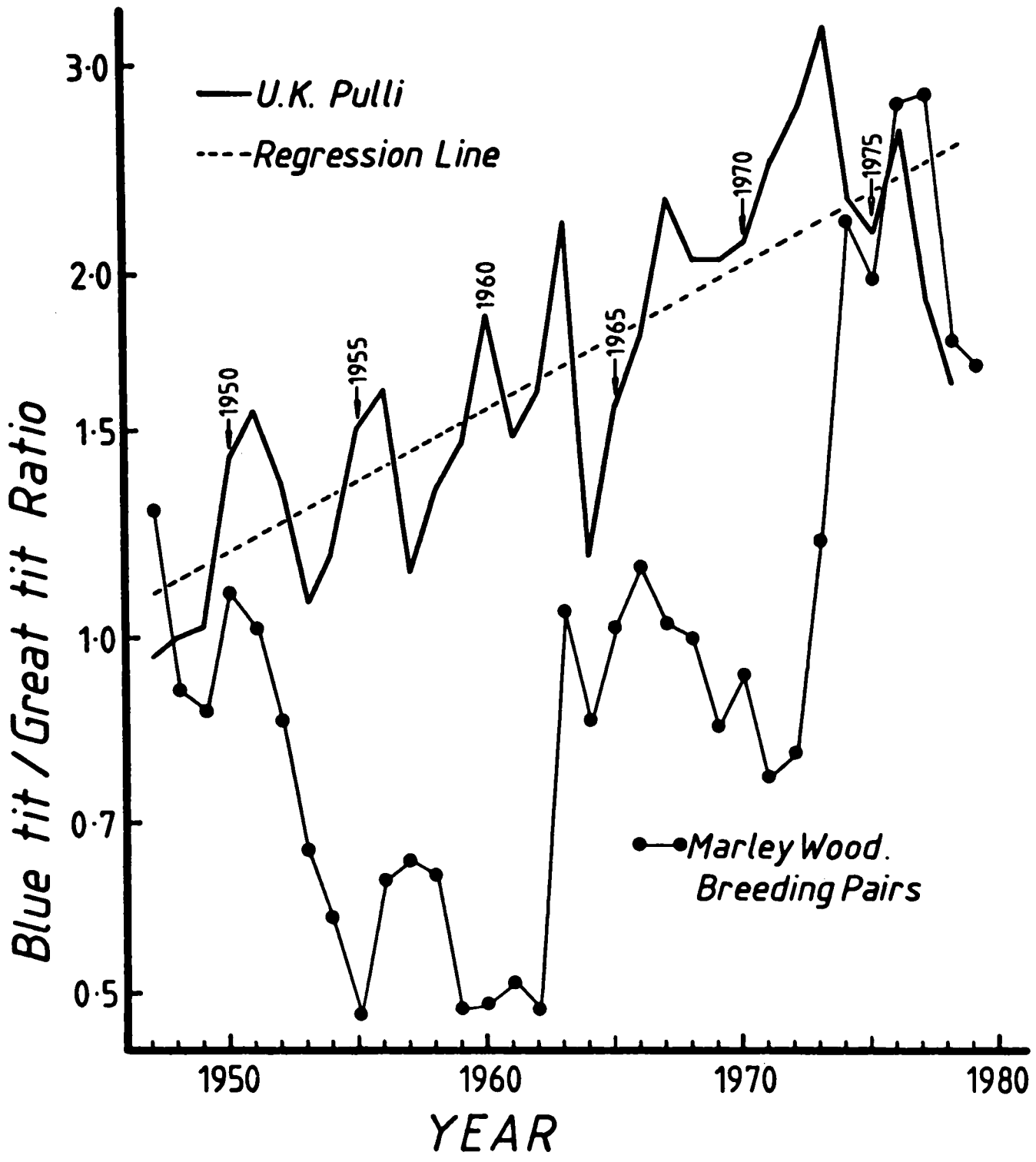


Figure 2.2 Changes in the ratio of the number of blue tits to the number of great tits over the last 30 years. The graph compares the ratios for pulli ringed in the U.K. with breeding pairs in Marley Wood.

given a choice. Before the 1973 breeding season 55 of the ca. 214 wooden boxes in Marley Wood were replaced by concrete boxes. If blue tit numbers were affected by the change in box type then there should have been an increased use of sites with concrete boxes after the change. This did not occur. For example, in 1971 blue tits used 24 of the unchanged sites and 12 of the sites later changed to concrete boxes (2.0:1). In 1974 blue tits used 51 of the unchanged sites and 20 of the changed sites (2.6:1). The selection of nest sites was apparently independent of box type (X^2_c = 0.11, n.s.). Thus the increase in blue tits is probably coincidental with, rather than caused by, the change to concrete boxes.

Each year the ca. 960 boxes in Wytham have been checked each week beginning about the time the first tits begin laying their eggs. The stage of nest construction or the number of eggs is noted at each weekly visit. The type of nest construction and, more particularly, the size of the eggs can be used to distinguish blue tit from great tit nests. These data are transferred from a field note book to nest record cards. The nest record cards form the basis of the permanent records for the tit breeding study in Wytham. The general rule has been to fill out a nest record card for each nesting attempt resulting in at least one egg. If one or both adults at a nest are captured the ring numbers are included on the card. Other data recorded are pertinent to chapters 5-7 and will be discussed there.

From the nest record cards it is possible to estimate the breeding populations of blue and great tits in each

section of Wytham. A count of all nest record cards would provide a biased estimate of breeding numbers because some nest records might be renestings. If both first and second attempts were recorded, there would be an overestimate of breeding numbers. This bias toward overestimation of numbers would be likely in sections of the wood or years with high predation where the loss of first nests resulted in second nesting attempts. Consequently, known or suspected renesting attempts were removed from the counts of breeding numbers. Occasionally, the same female has been caught at two different nests. In such cases the second nest is known to be a renesting attempt. More often, a nest is started which is either abandoned or predated, and then a late nest is started in a box close to the first. Such instances of a nest being started near to and after a nest that failed have also been recorded as repeat nests and not included in the estimate of the number of breeding pairs.

Key-factor analysis

The term 'key-factor' was first used by Morris (1959) to refer to any factor related to mortality that resulted in a change of population density from generation to generation. Morris (1963) expanded the meaning to include "any factor that is useful in the prediction of population changes, with no comment as to the precise mode of operation of the factor". Despite the general definition of a key-factor, Morris proposed a specific method of analysis. For a population studied over a number of years (or generations) he regressed the log density in

one year (N_{t+1}) against the log density in the preceding year (N_t). He then tried to account for the density dependent effects of mortality factors until the regression line approached a slope of one. Finally, he tested whether residual variation was correlated with density independent factors such as weather. Morris (1963) recognised that multiple regression might be more appropriate as a technique for his basic model.

Varley and Gradwell (1960) presented a graphical method of examining the components of total generation mortality (K) as a series of mortality factors (k_i) at different stages in the life cycle of a population. The mortality factors were considered to act sequentially so that mortality, k_i, for the ith factor could be defined as the difference between the log number of individuals at the beginning and end of the ith period of time in the life cycle. Because they used the log of mortality at each stage, $K = \Sigma k_i$. Varley et al. (1973) defined the term key-factor to mean any factor causing, rather then useful in predicting, population change. However, Varley et al. also used key-factor to refer to periods in the life cycle in which large changes occurred (e.g. winter disappearance). I prefer to keep to Morris' (1963) definition as the least presumptuous and most useful. Further, it is not always possible to partition mortality caused by one factor into a discrete period of time.

Does interspecific competition cause changes in either the blue tit or great tit population? While this would be the ideal question to answer it is necessary to

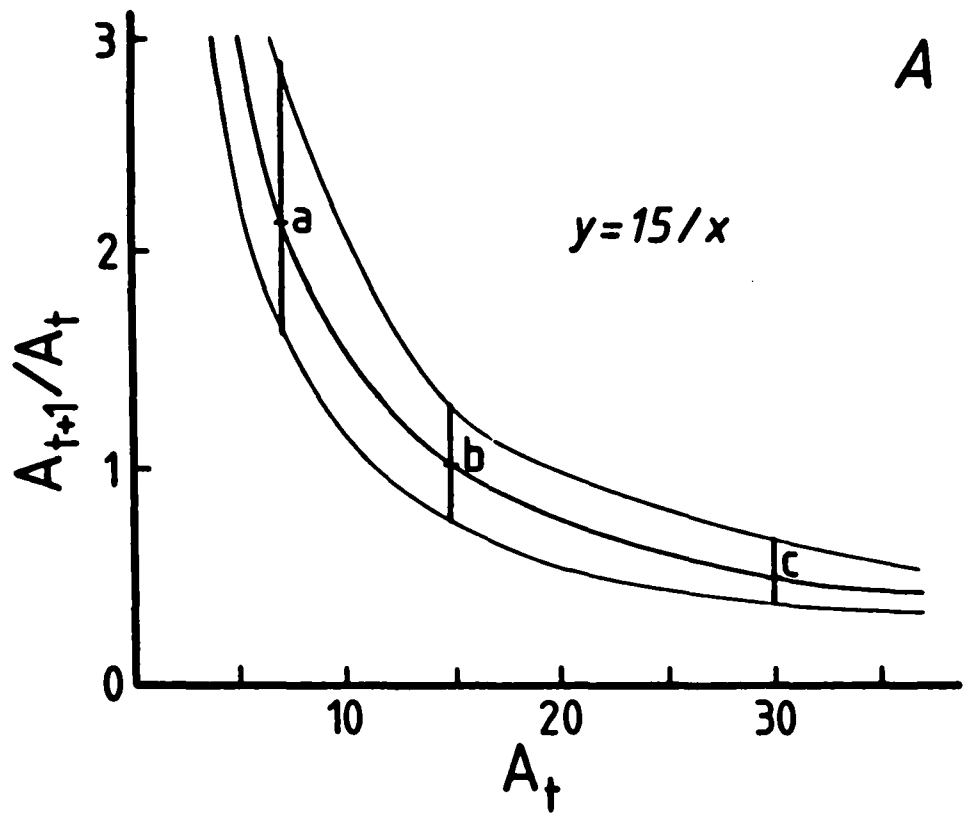
settle for asking whether the density of blue tits is useful in predicting changes in the number of great tits (or vice versa). If the magnitude of interspecific competition is related to the survival of a certain species then a large number of competitors should depress that species' population level more than a small number of competitors. To test whether this occurs in blue and great tits, it is necessary to develop a key-factor model.

Assuming that a population of species A fluctuates within an upper and lower limit then its population in any year t (A_t) should provide a predictor for the change to the following year (A_{t+1}/A_t). This relationship is the essence of what Royama (1977) termed statistical density dependence. The density A_t at which A_{t+1}/A_t is expected to be one (1.0) may be thought of as the equilibrium, whether or not it is a stable point. It is helpful to think of the equilibrium as fixed when considering a return to the equilibrium in year t+1 following a perturbation in year t. The relationship between A_t and A_{t+1}/A_t will not be linear (Figure 2.3A). However, $\log_e$ transformations of both A_t and A_{t+1}/A_t make the relationship linear (Figure 2.3B). The $\log_e$ transformations have the further advantage of tending to equalize the variance of $\ln(A_{t+1}/A_t)$ across all $\ln(A_t)$ and thus make the use of linear regression more legitimate in estimating the equilibrium. A regression model for the return to equilibrium would be

$$\ln(A_{t+1}/A_t) = a_1 \ln(A_t) + a_0 \quad *.$$

However, without being able to distinguish perturbations from a return to the equilibrium the model is based on

*where a_0 and a_1 are regression coefficients



Figures 2.3 A&B Hypothetical model in which a population with a density A_t in year t returns to an equilibrium density of 15 following a change in density. Assuming a 25 percent error in the equilibrium value the thin lines show the variance about the function and the horizontal bars show the variance at three points on the graph. 'A' shows the untransformed function and 'B' the transformed function.

wholly circular reasoning. We can ascribe little meaning to a_1, whether or not it is statistically significant.

It is possible to include probable sources of perturbation into the model as well as the expected return to equilibrium. It may be useful to think of factors other than the number of species A as affecting the equilibrium density of species A. Thus, as external factors change, such as the population density of a competing species, winter severity, or food supply, they cause the population to 'chase' a new equilibrium point. Because A_t is expected to have some correlation with A_{t+1}/A_t on a priori grounds, a conservative approach to testing the significance of the sources of perturbation is to use a step-up multiple regression model in which A_t is the first term to be included and additional terms are added step wise. This procedure will reduce the likelihood of including a factor in the model because of chance correlation with A_t. This is particularly important in assessing the significance of the population density of a competing species (B_t) because A_t and B_t could be correlated through parallel responses of both populations to common external influences (e.g., weather, food, habitat changes, etc.).

RESULTS AND DISCUSSION

Breeding numbers in Wytham Woods

The basic population data for Wytham consist of the number of breeding pairs of blue and great tits in each of the eight sections of the Wood. For Marley Wood these are given for 1947 to 1979 in Table 2.2. For all eight sections

Table 2. 2 . Number of breeding pairs of blue and great tits in Marley Wood from 1947 - 1979. Also included are the means of the daily minimum temperatures in March (°C) and the Dutch beech mast index (estimated for 1976 - 1979). The beech mast index was calculated by the Dutch Forest Service for trees in Holland.

YEAR	GREAT TIT	BLUE TIT	MARCH TEMP	BEECH CROP
1947	7	9	1.33	20
1948	21	19	3.44	78
1949	30	26	1.67	19
1950	31	34	3.56	39
1951	32	34	1.61	27
1952	20	17	3.89	29
1953	21	14	0.28	39
1954	31	18	2.83	29
1955	27	13	-0.44	21
1956	24	15	2.22	76
1957	49	32	5.94	16
1958	27	17	0.94	61
1959	41	20	4.06	21
1960	51	25	3.83	77
1961	86	44	3.67	21
1962	43	21	-0.67	22
1963	39	41	3.00	21
1964	54	46	2.11	42
1965	46	47	1.78	27
1966	45	52	3.22	24
1967	32	33	4.22	35
1968	33	33	3.61	49
1969	38	32	1.17	23
1970	30	28	0.67	66
1971	46	35	2.22	28
1972	36	29	2.78	36
1973	39	47	2.11	38
1974	26	58	2.27	62
1975	32	64	2.56	27
1976	14	39	1.72	>50
1977	30	85	4.28	<50
1978	26	46	3.33	<50
1979	19	32	2.11	<50

of the Wood from 1958 to 1979, the numbers are in Tables 2.3 and 2.4. Because each section is a different size, the numbers are converted to densities in Tables 2.5 and 2.6. These data will provide the core for discussion and analysis throughout most of this chapter. In comparing different sections of the wood, I shall use the data for 1964 to 1979. This allows full factor analysis of species, year and section of the wood. Many of the analyses were repeated using the data for 1958 to 1979, adjusting for missing values by using values that minimized the error mean square in an analysis of variance. Reassuringly, I obtained very similar results from those analyses, but the adjustment for missing values causes interpretational difficulties for many of the analyses. Consequently, I shall limit my discussion to the data for 1964 to 1979 where the effect of area of the Wood is of interest or where replicates of species or year are required.

The data for the eight sections, 16 years and two species provide an opportunity to look at three factors possibly related to breeding density. A full factorial analysis of variance shows the effect of these factors on breeding density (Table 2.7). Because there is no full factor replication, the three-way interaction term was used as the error term and cannot be tested. All three main factors were significant. During the 16 years the average density of blue tits has been higher than for great tits. Bean Wood has had the highest breeding densities of tits and Extra the lowest densities. Breeding densities were very high in 1975 and 1977 and low in 1968 and 1969. There

Table 2.3. Number of breeding pairs of blue tits in eight sections of Wytham Wood 1958-1979. Numbers in parentheses are thought to be low.

BLUE TITS

	B	W	O	E	CP	C	MP	SW
1958	17	27	(6)	-	-	-	-	-
1959	20	40	21	31	12	-	-	-
1960	25	43	33	30	16	-	-	-
1961	44	55	30	31	16	(27)	-	-
1962	21	22	20	20	10	20	28	-
1963	41	20	21	30	10	25	39	(23)
1964	46	18	15	22	7	34	34	46
1965	47	14	32	31	6	30	20	49
1966	52	36	42	34	9	37	33	48
1967	33	30	41	43	15	33	28	37
1968	33	27	33	31	7	34	21	31
1969	32	22	34	31	12	47	26	34
1970	28	27	26	43	16	46	18	40
1971	35	40	42	48	20	44	22	47
1972	29	25	38	54	16	34	23	21
1973	47	35	38	56	22	36	34	36
1974	58	44	66	65	22	51	40	46
1975	64	75	69	72	24	52	50	46
1976	39	45	40	65	23	38	33	37
1977	85	61	72	71	25	65	55	66
1978	46	47	60	71	24	47	41	47
1979	33	43	45	61	19	35	35	32

Table 2.4. Number of breeding pairs of great tits in eight sections of Wytham Wood 1958-1979. Numbers in parentheses are thought to be low.

	GREAT TITS							
	B	W	O	E	CP	C	MP	SW
1958	27	17	(11)	-	-	-	-	-
1959	41	22	26	36	11	-	-	-
1960	51	21	22	47	6	-	-	-
1961	86	37	42	51	19	(21)	-	-
1962	43	23	31	43	9	20	15	-
1963	39	17	30	43	7	16	11	(5)
1964	54	34	45	49	13	35	14	21
1965	46	27	35	48	11	30	15	27
1966	45	13	32	34	15	22	13	23
1967	32	12	20	22	8	14	7	16
1968	33	14	21	39	13	14	14	20
1969	38	19	24	41	11	16	14	24
1970	30	12	19	21	5	15	15	12
1971	46	27	30	39	12	21	21	29
1972	36	18	18	35	8	18	25	16
1973	39	29	16	29	10	15	19	21
1974	26	21	15	21	6	18	17	17
1975	32	28	14	28	10	27	16	19
1976	14	15	20	27	6	14	17	7
1977	30	31	27	46	17	29	19	27
1978	26	16	25	32	12	22	14	24
1979	19	15	26	36	14	18	13	20

Table 2.5. Density (pairs ha^{-1}) of breeding blue tits in eight sections of Wytham Wood from 1958-1979. Numbers in parentheses are thought to be low.

	BLUE TITS							
	B	W	O	E	CP	C	MP	SW
1958	0.64	1.04	(0.17)	-	-	-	-	-
1959	0.75	1.54	0.59	0.51	0.63	-	-	-
1960	0.94	1.66	0.93	0.49	0.84	-	-	-
1961	1.65	2.12	0.84	0.51	0.84	(1.59)	-	-
1962	0.79	0.85	0.56	0.33	0.53	1.18	1.50	-
1963	1.54	0.77	0.59	0.49	0.53	1.47	2.09	(0.85)
1964	1.72	0.69	0.42	0.36	0.37	2.00	1.83	1.70
1965	1.76	0.54	0.90	0.51	0.32	1.76	1.07	1.81
1966	1.95	1.39	1.18	0.56	0.47	2.18	1.77	1.77
1967	1.24	1.16	1.15	0.71	0.79	1.94	1.50	1.36
1968	1.24	1.04	0.93	0.51	0.37	2.00	1.13	1.14
1969	1.20	0.85	0.95	0.51	0.63	2.76	1.40	1.25
1970	1.05	1.04	0.73	0.71	0.84	2.71	0.97	1.48
1971	1.31	1.54	1.18	0.79	1.05	2.59	1.18	1.73
1972	1.09	0.97	1.07	0.89	0.84	2.00	1.24	0.77
1973	1.76	1.35	1.07	0.92	1.16	2.12	1.83	1.33
1974	2.17	1.70	1.85	0.99	1.16	3.00	2.15	1.70
1975	2.40	2.90	1.94	1.19	1.26	3.06	2.69	1.70
1976	1.46	1.74	1.12	0.99	1.21	2.24	1.77	1.36
1977	3.18	2.36	2.02	1.17	1.31	3.82	2.95	2.43
1978	1.72	1.81	1.68	1.17	1.26	2.76	2.20	1.73
1979	1.24	1.66	1.26	1.00	1.00	2.06	1.88	1.18

Table 2.6. Density (pairs ha^{-1}) of breeding great tits in eight sections of Wytham Wood from 1958-1979. Numbers in parentheses are thought to be low.

GREAT TITS

	B	W	O	E	CP	C	MP	SW
1958	1.01	0.66	(0.31)	-	-	-	-	-
1959	1.54	0.85	0.73	0.59	0.58	-	-	-
1960	1.91	0.81	0.62	0.77	0.32	-	-	-
1961	3.22	1.43	1.18	0.84	1.00	(1.24)	-	-
1962	1.61	0.89	0.87	0.71	0.47	1.18	0.81	-
1963	1.46	0.66	0.84	0.71	0.37	0.94	0.59	(0.18)
1964	2.02	1.31	1.26	0.81	0.68	2.06	0.75	0.77
1965	1.72	1.04	0.98	0.79	0.58	1.76	0.81	1.00
1966	1.68	0.50	0.90	0.56	0.79	1.29	0.70	0.85
1967	1.20	0.46	0.56	0.36	0.42	0.82	0.38	0.59
1968	1.24	0.54	0.59	0.64	0.68	0.82	0.75	0.74
1969	1.42	0.73	0.67	0.68	0.58	0.94	0.75	0.89
1970	1.12	0.46	0.53	0.35	0.26	0.88	0.81	0.44
1971	1.72	1.04	0.84	0.64	0.63	1.24	1.13	1.07
1972	1.35	0.69	0.51	0.58	0.42	1.06	1.34	0.59
1973	1.46	1.12	0.45	0.48	0.53	0.88	1.02	0.77
1974	0.97	0.81	0.42	0.35	0.32	1.06	0.91	0.63
1975	1.20	1.08	0.39	0.46	0.53	1.59	0.86	0.70
1976	0.52	0.58	0.56	0.44	0.32	0.82	0.91	0.26
1977	1.12	1.20	0.76	0.76	0.89	1.71	1.02	1.00
1978	0.97	0.62	0.70	0.53	0.63	1.29	0.75	0.89
1979	0.71	0.58	0.73	0.59	0.74	1.06	0.70	0.74

Table 2.7 . Analysis of variance of density of breeding pairs of tits in Wytham Wood. Main factors are species, section of the wood, and year. The three-way interaction is used for the error term. DF is degrees of freedom, SS% is the percentage sum of squares, and MS is the mean square. Interactions are indicated by a dot, e.g., SECTION·YEAR

SOURCE OF VARIATION	DF	SS%	MS	F-RATIO	P<
SPECIES	1	24.83	24.882	378.09	0.001
SECTION	7	32.30	4.623	70.25	0.001
YEAR	15	12.17	0.813	12.35	0.001
SECTION·SPECIES	7	6.08	0.871	13.23	0.001
SPECIES·YEAR	15	10.91	0.729	11.07	0.001
SECTION·YEAR	105	6.81	0.065	0.99	n.s.
Residual	105	6.90	0.066		
TOTAL	255	100.00			

were two significant interactions. The interaction between area and species was largely caused because the difference between the density of blue tits and great tits in Bean Wood was much larger than in the other areas. The interaction between species and year was most noticeable in 1964 when there were more great than blue tits and 1975 and 1977 when there were many more blue than great tits. It may be argued that both interaction terms would be expected to be multiplicative rather than additive. The use of log transformed densities in an otherwise identical analysis of variance does reduce the percentage sum of squares for the area - species interaction from 6.3 to 2.4, but the term is still highly significant ($F_{7,105} = 3.45$, $P < 0.005$). The absence of a significant interaction between area and year must be viewed cautiously in the absence of a three-way interaction term. The analysis of variance shows that year, species, and section of the wood, or factors related to them, are associated with and probably affect the breeding densities of tits in Wytham.

The analysis of variance on breeding density may pick out systematic changes in density over the entire 16 year period. The ~~log~~ $\log_e$ change in density from one year to the next ($R_t = \ln(N_{t+1}/N_t)$) may be used as a variate in place of density. The analysis of variance should then measure the effect of year and the year interactions independent of long term changes in density caused by, for example, changes in habitat. Section of the woods, species, and the species - section interaction should have no effect and are treated as error strata in the analysis. Again,

year and the year - species interaction were highly significant sources of variation, while the section - year interaction was not significant (Table 2.8). The analysis leaves the problem of why the tit numbers increase or fall in certain years and why the two species react differently to effects brought about over the same years.

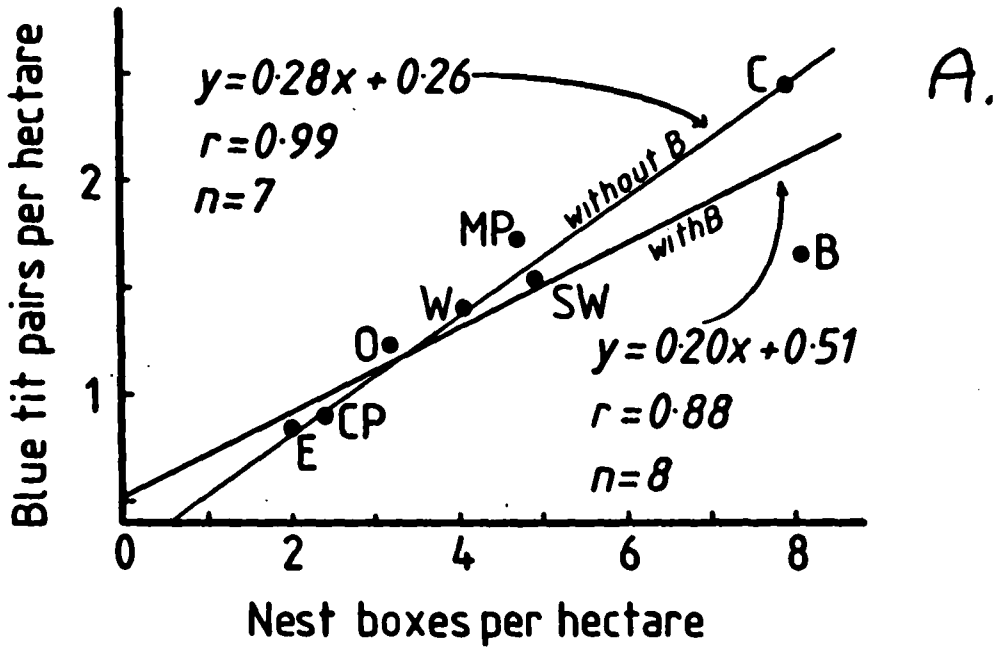
The analyses of variance have shown that breeding densities and changes in breeding densities are associated with several factors which interact with each other. Essentially, the analyses show that there are problems that require solving or significant effects that need an explanation. In the rest of this chapter I shall investigate some of these problems using the 1949 to 1979 data for Marley Wood and the 1964 to 1979 data for the whole of Wytham.

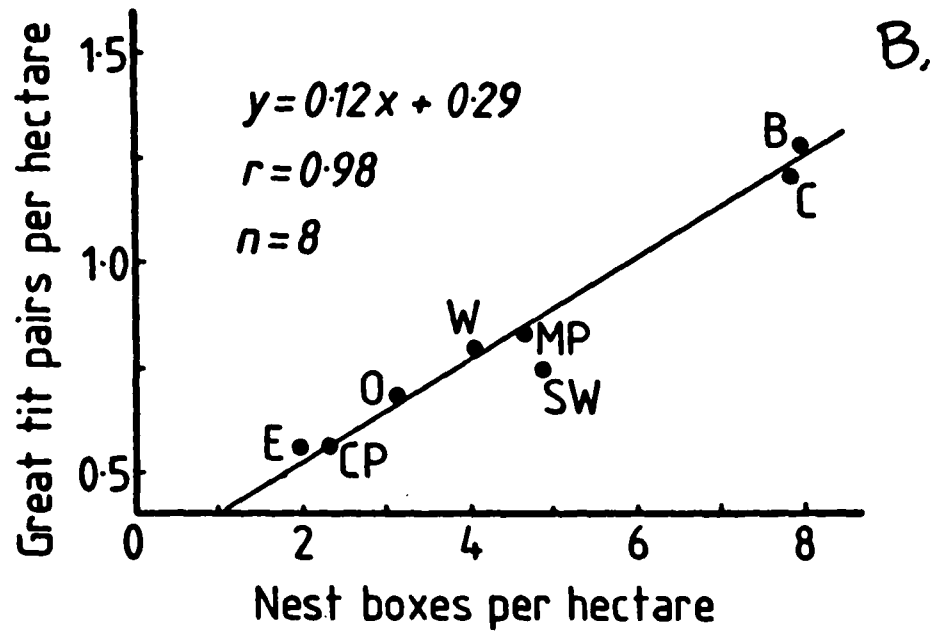
Does the density of boxes limit the number of breeding tits?

If the density of boxes in a section of the woods is limiting the density of breeding birds, then there should be a correlation between box density and breeding density at least in years of high density. Unfortunately, the only measure of breeding density that is available for Wytham is the number of birds breeding in boxes. Both blue and great tits show a high correlation between breeding density in boxes and nest-box density in the eight sections of Wytham (Figure 2.4). The one exception is the density of blue tits in Marley. There are two likely explanations for this anomaly. First, boxes in Marley tend to be more clumped in their distribution compared with the other seven sections of the wood. This would have a greater effect on blue tits

Table 2. 8 . Analysis of variance of the log change in breeding numbers from one year to the next in each section of Wytham. Species, section of the wood, and the species - section interaction are treated as block error strata. DF is degrees of freedom, SS% is percentage sum of squares, MS is mean square.

SOURCE OF VARIATION	DF	SS%	MS	F-RATIO	P<
SECTION STRATUM	7	0.43	0.021	0.27	
SPECIES STRATUM	1	0.56	0.192	2.50	
SECTION·SPECIES STRATUM	7	0.34	0.017	0.22	
SECTION·SPECIES·UNITS STRATUM					
YEAR	14	44.75	1.091	13.93	0.001
SECTION·YEAR	98	16.54	0.058	0.74	n.s.
SPECIES·YEAR	14	14.89	0.363	4.64	0.001
Residual	98	22.49	0.078		
TOTAL	224	98.66	0.150		
GRAND TOTAL	239	100.00			





Figures 2.4 A&B Relationship between nest-box density and mean density of breeding blue tits (A) and great tits (B) in eight sections of Wytham Woods (1964 - 1979). *Abbreviations for section of the wood are given in Table 2.1, p15. For blue tits the regression line is given both with and without the data for Marley Wood (B).*

which have smaller territories than great tits. Second, the habitat in Marley may differ from other areas, being unfavourable to blue tits but not great tits. Marley does have a considerable area of coppiced hazel and actual open spaces as well as second growth woods more favourable to great tits than the open oak woodlands preferred by blue tits. Lack (1966:13) also concluded that Marley was less favourable to blue tits than woods with a higher proportion of oaks, including much of the rest of Wytham. In addition, the greatest density of nest boxes tend to be in areas less favourable to blue tits. The net result of these two points is that blue tits may encounter a lower apparent or effective density of boxes, there being fewer boxes available within suitable habitat or potential territories. If blue tits in Marley were acting as blue tits in other areas, their mean breeding density would have been nearer 2.5 pairs ha^{-1} than the 1.65 pairs ha^{-1} observed.

It is somewhat puzzling that the relationship between nest-box density and breeding density should be so linear when the slopes are much less than one. Clearly, not all boxes are used for breeding in years with an average breeding density. Part of the explanation is that the fluctuating densities of breeding birds means that only in very high density years is the maximum breeding density (= nest-box density) approached in the high box density areas, while it is approached during moderate density years in the low box density areas. This is probably true more for great tits than blue tits as will be discussed later. It may be that if the nest-box density in Marley or Bean

Wood is doubled, the breeding density of blue and great tits may both exhibit an asympotic mean breeding density.

I said that this explanation was only part of the answer. It will be shown below that at least for blue tits, the sections of the Wood with higher densities of blue tits have smaller fluctuations in breeding numbers. This could result from habitat differences between sections of the wood as well as differences in competition for boxes caused by box density. These possibilities will be discussed later, but for now it is noteworthy that the variance of the $\log_e$ density of blue tits in Marley ($s^2_{ln} = 0.097$) is higher than in Bean Wood ($s^2_{ln} = 0.045$; $F_{15,15} = 0.097/0.045 = 2.15$; $P < 0.05$, one-tailed) which has almost the same density of boxes as Marley. This result would be expected if the blue tits encounter a lower effective density of boxes in Marley than would be expected from the actual density present.

Finally, it should be noted that the slope for great tits is not as steep as for blue tits (Figure 2.4). As the density of boxes increased, there were relatively more blue tits than great tits. There are two likely explanations for this. First, blue tits have smaller territories than great tits so that increasing the number of boxes allows more blue tits than great tits room to breed. Thus, great tits should be relatively better off at the lower densities of nest boxes. Secondly, at the lower densities of nest boxes great tits may actually suppress the number of breeding blue tits by taking the boxes during high breeding density years, whereas blue tits experience a competitive

release in high nest box density sections of the wood and in years of low breeding densities. The evidence supporting the second explanation is presented later in this chapter and in Chapter 3.

The abundance of artificial nest sites probably has a real effect on the breeding densities of blue and great tits at least within limits. Kluijver (1951) and Gibb (1954) found that virtually all great tits and most blue tits used artificial nest boxes. Kluijver (1951) and Higuchi (1978) both found that increasing the number of nest boxes increased the breeding density of great tits. Before confidently extending these results to blue tits it will be necessary to experimentally manipulate the number of nest boxes available in a wood and census the number of breeding birds in years of high and low densities of boxes. However, it is likely that the availability of artificial sites has had a significant effect on the number of breeding blue tits as well as great tits.

Effect of nest-box density on annual changes in blue and great tit density

The changes in blue tit numbers and changes in great tit numbers (log ratio of numbers in year n+1 divided by numbers in year n) were highly correlated in Marley Wood ($r=0.74$, $n=15$, $P< 0.001$). In no other section of Wytham was the correlation as high. One reason for this drop in correlation may be the density of boxes provided in the various sections of the wood. Figure 2.5 shows a plot of box density against the correlation coefficient for changes in breeding density in the eight sections of the wood. The

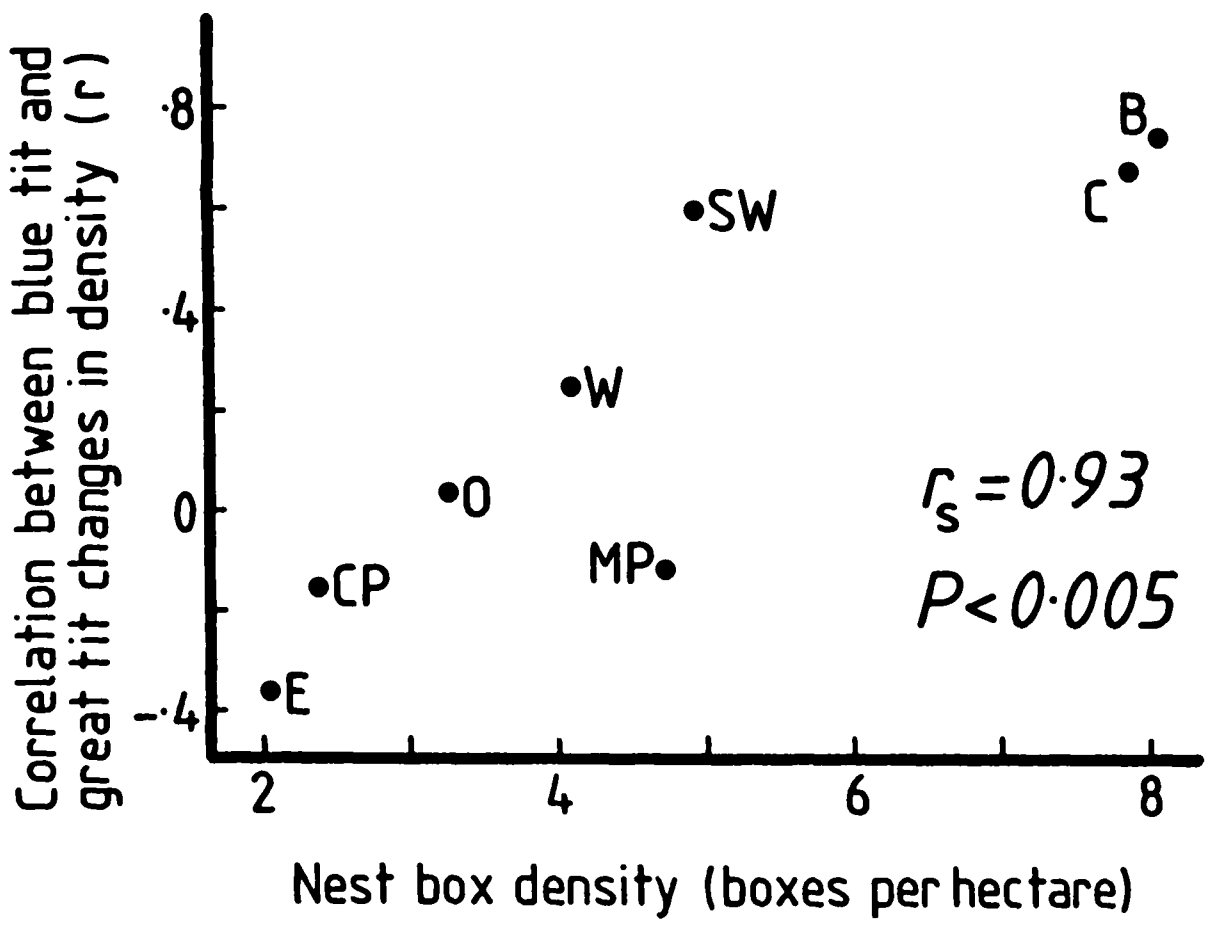


Figure 2.5 Effect of nest-box density on the correlation coefficient (r) between blue tit and great tit log changes in density (R_t) in eight sections of Wytham Woods (1964 - 1979).

increase in correlation with box density is significant (Spearman rank correlation, $r_s = 0.93$, $P < 0.005$). This is probably a result of competition for the boxes between blue and great tits. Apparently, what happens is as follows. Great tits are dominant in contests for nest boxes. Even in years with conditions favouring both blue and great tits, there are enough boxes for both species in sections of the wood with a high density of boxes. Areas with an intermediate density of boxes can accommodate most individuals of both species in boxes only in years of moderate density. In fact, if the density of boxes is very low, there may even be an inverse relationship between the changes in blue tit and great tit density, as occurred in Extra. The combined blue and great tit breeding densities have reached 5.5 and 4.8 pairs ha^{-1} in Bean Wood and Marley Wood respectively. Thus, the apparent shortage of boxes in sections like Common Piece and Extra is probably real. In an average year 60% of the boxes in Common Piece and Extra have been used and in years with a high breeding density over 95%. This compares with an average of 37% and a high of 60% in Marley Wood.

Relationships between breeding density and the variation in breeding numbers

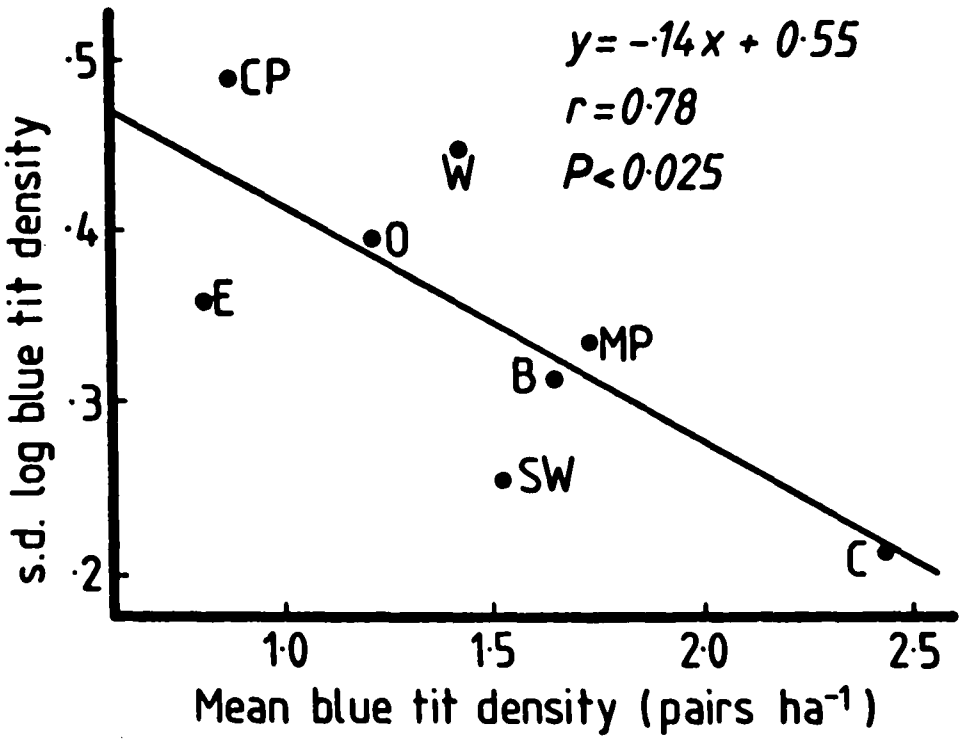
Comparisons between sections of the wood

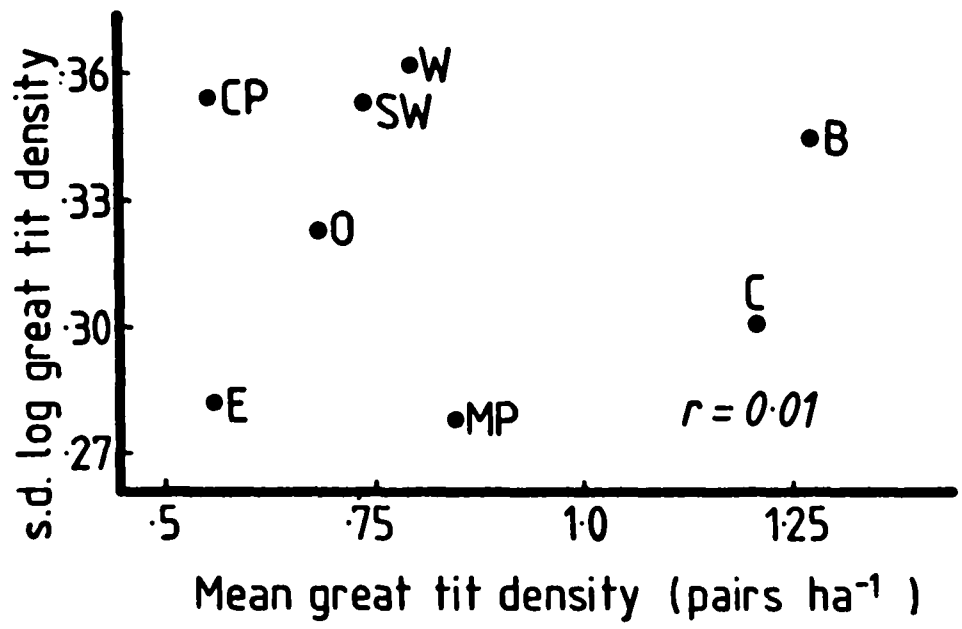
As the breeding density of tits changes it may be that the variation in density between sections of the wood or between years also changes. The standard deviation of density as an untransformed variate is not a good measure of variation because the standard deviation would be

expected to increase at higher densities. However, the $\log_e$ transformed densities should have a constant standard deviation if the amount of relative variation is constant for all breeding densities. The standard deviation of log density is the square root of the variance of $\log_e$ density ($S^2_{ln}(N_t)$). The variance of log density has been used as a measure of population stability by Wolda (1978). Taylor and Woiwod (1980) found that for a number of insect species the variance of $\log_e$ density for a population was dependent on the mean density of the population. Thus, for interdemic comparisons the standard deviations of $\log_e$ density might not be expected to be equal at all mean densities. However, the tits in Wytham are all part of the same population and probably should be considered a sub-population of a larger population which includes the surrounding woods and copses.

Differences between sections of Wytham were examined by calculating the mean breeding density and standard deviation of $\log_e$ density for each section and species. Thus, each mean and standard deviation is based on 16 years of breeding densities. The standard deviation of $\log_e$ blue tit density had a significant negative correlation with the mean densities of blue tits in the eight sections of the wood. However, there was no such relationship for great tits (Figure 2.6).

The negative relationship for blue tits, taken on its own, is a bit surprising. It might have been expected to be a positive relationship. Because areas with the highest densities of blue tits have had the greatest den-





Figures 2.6 A&B Effect of breeding density of blue tits (A) and great tits (B) on the standard deviation (s.d.) of $\log_e$ breeding density in eight sections of Wytham (1964 - 1979). For abbreviations see Table 2.1, p.15.

sities of boxes, those areas should accomodate much higher densities of blue tits in years of overall high populations, whereas in areas with a low density of boxes most boxes should be used in all years. The negative relationship for blue tits could result from two possible causes. One possibility is that the areas with low densities of nest boxes happen to be the poorest habitats. Blue tits might only move into those sections when high numbers in other sections forced the breeding surplus into the marginal habitats. If this were the whole story, then there should still be a reasonably high correlation between changes in blue tit numbers in high blue tit density areas, like Bean Wood, Marley Wood, and Marley Plantation, with changes in low blue tit density areas like Extra and Common Piece. This was not the case (Table 2.9), although it was generally true for great tits (Table 2.10). The second possibility is that competition for nest sites results in fewer blue tits in the low density areas getting nest boxes in years when both blue and great tit populations increase in the higher density sections of the woods. If this was true, then the correlations between changes in blue tit numbers with changes in great tit numbers should be high for high density areas and low for low density areas. This was generally true (Table 2.11).

Instead of looking at the variance of the two species independently, the standard deviation of the $\log_e$ ratio of blue tits to great tits may be used. As might be expected the variances for the eight sections were closely related to the densities of both blue ($r = -.80$) and great ($r = -.64$)

Table 2. 9 . Correlations between changes in blue tit numbers from year to year ($\ln(N_{t+1}/N_t)$) in eight sections of Wytham Wood.

B	-							
W	.61	-						
O	.66	.41	-					
E	.22	.26	.53	-				
CP	.12	.38	.16	.53	-			
C	.79	.56	.58	.17	.32	-		
MP	.71	.70	.40	.09	.44	.70	-	
SW	.79	.57	.53	.27	.38	.73	.46	-
	B	W	O	E	CP	C	MP	SW

Table 2. 10. Correlations between changes in great tit numbers from year to year ($\ln(N_{t+1}/N_t)$) in eight sections of Wytham Wood.

B	-							
W	.78	-						
O	.34	.44	-					
E	.60	.72	.63	-				
CP	.83	.72	.57	.83	-			
C	.83	.71	.59	.59	.66	-		
MP	.26	.26	.42	.67	.42	.36	-	
SW	.92	.81	.45	.69	.85	.78	.26	-
	B	W	O	E	CP	C	MP	SW

Table 2. 11. Correlations between changes in blue tit and changes in great tit numbers ($\ln(N_{t+1}/N_t)$) in eight sections of Wytham Wood.

BLUE TITS	B	W	O	E	CP	C	MP	SW
B	.75	.67	.30	.44	.68	.75	.26	.75
W	.52	.26	.17	.07	.53	.43	-.06	.40
O	.53	.36	.67	.24	.40	.57	.03	.67
E	.21	.02	-.44	-.37	-.16	.23	-.37	.11
CP	.15	.10	-.04	-.42	-.14	.00	-.64	.03
C	.60	.44	.26	.20	.41	.68	.09	.58
MP	.64	.48	.22	.23	.58	.54	-.11	.53
SW	.54	.55	.41	.16	.41	.54	-.02	.61

GREAT TITS

tits as well as to the density of boxes ($r = -.74$). The best fit for predicting the variance of the $\log_e$ ratio came from a combination of box density and great tit density. Interestingly, the relationship between the variance and great tit density was positive after correcting for box density, although it was not significant (Table 2.12).

Variations between years

The same relationships between breeding density and variation in the density of the two species may be studied between years rather than between sections of the wood. The variation in density was measured as the standard deviation of $\log_e$ density for eight sections, i.e., the total number of each species for the year divided by the total area of the woods. If the availability of nest sites for blue tits was affected by the breeding density of great tits but not vice versa, then the comparisons between years should produce results similar to the results for comparisons between sections of the wood. That is, the standard deviation of the $\log_e$ of great tit density may have a weak relationship with great tit breeding density, but the standard deviation of $\log_e$ blue tit density should be negatively related to blue tit density and positively related to great tit density. This is, in fact, the case. The correlation between great tit density and the standard deviation of $\log_e$ great tit density was negative, but not significant ($r = -0.30$). Adding blue tit density did not explain any additional variation in the standard deviation of $\log_e$ great tit density. The correlation between blue tit density and the standard deviation of $\log_e$ blue tit

Table 2.12 . Effect of great tit density and box density on the standard deviation of the log$_e$ ratio of blue to great tit density in eight sections of Wytham from 1964 to 1979. The two variates explain 62 percent of the variance in the independent variable.

	Coefficient	t-test	P<
Constant	0.400	2.34	0.10
Box density	-0.156	2.40	0.10
Great tit density	0.987	1.81	0.20

density was negative ($r = -0.44$, $n = 16$, $P < 0.10$). The addition of $\log_e$ great tit density explained much of the residual variation in the standard deviation of $\log_e$ blue tit density not explained by blue tit density (Table 2.13). In fact, great tit density alone explained 40.4 percent of the variance in the standard deviation of $\log_e$ blue tit density ($r = 0.69$, $n = 16$, $P < 0.005$). Again, the most reasonable interpretation is that in years with high densities of great tits the blue tits are restricted from making proportional fluctuations in all eight sections. As great tit densities increase, blue tits can only increase in sections of the wood with high densities of nest boxes. In years when the blue tits have achieved a high density throughout the wood then the variance of log blue tit density has been low. The significance of blue tit density can be detected even when partialling out the effect of great tit density. This is because of the low correlation between blue and great tit numbers throughout the woods ($r = 0.04$). Thus, the effects of the densities of the two species are virtually orthogonal with respect to the multiple regression in Table 2.13.

Box density and competition for boxes: Marley vs Common Piece

I have already shown that the correlation between blue tit and great tit numbers in Wytham varies between sections of the wood according to the density of nest boxes available. I suggested that this could be because great tits were dominant over blue tits. If great tits tended to take the boxes that might otherwise have been used by

Table 2.13 . Effects of blue tit and great tit densities on the standard deviation in $\log_e$ blue tit density in eight sections of Wytham Woods. Data are for the 16 years from 1964 to 1979. The two variates explain 54.5 percent of the variance.

	Coefficients	t-test	P<
Constant	0.225	1.43	n.s.
Blue tit density	-0.132	2.27	0.05
Great tit density	0.432	3.62	0.005

blue tits then a comparison of the great tit - blue tit ratio in a high box density section like Marley with the great tit - blue tit ratio in a low box density area like Common Piece, should show that relative to Marley, the ratio in Common Piece decreases as the general population of great tits increases. An increase in the population of blue tits should have little, or perhaps a slightly negative, relationship with the ratio in Common Piece relative to Marley. This is, in fact, the case (Figure 2.7A). The contribution of blue tit numbers was not significant. The result is consistent with the prediction. However, it could be that the ratio of numbers of great tits in Marley to great tits in Common Piece decreased when the numbers of great tits increased. It is easier to see this by noting the equality

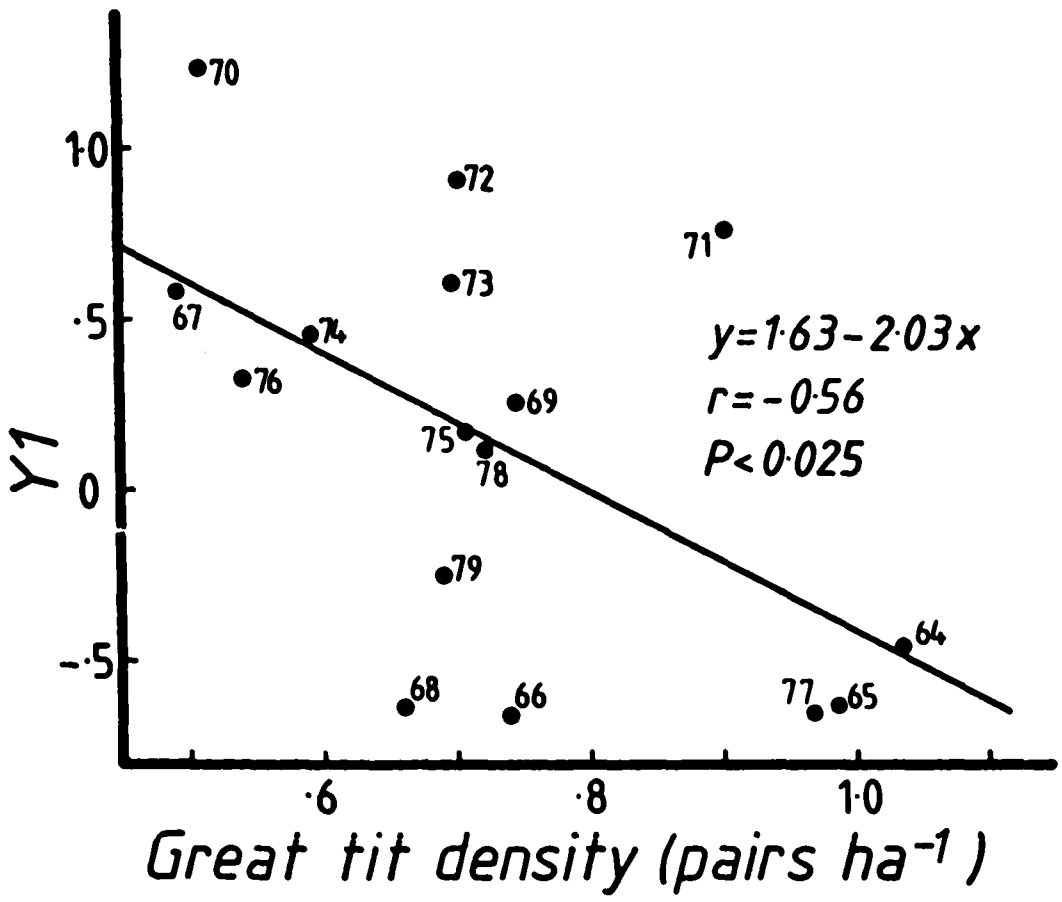
$$(GT_B/BT_B)/(GT_{CP}/BT_{CP}) = (GT_B/GT_{CP})/BT_B/BT_{CP}).$$

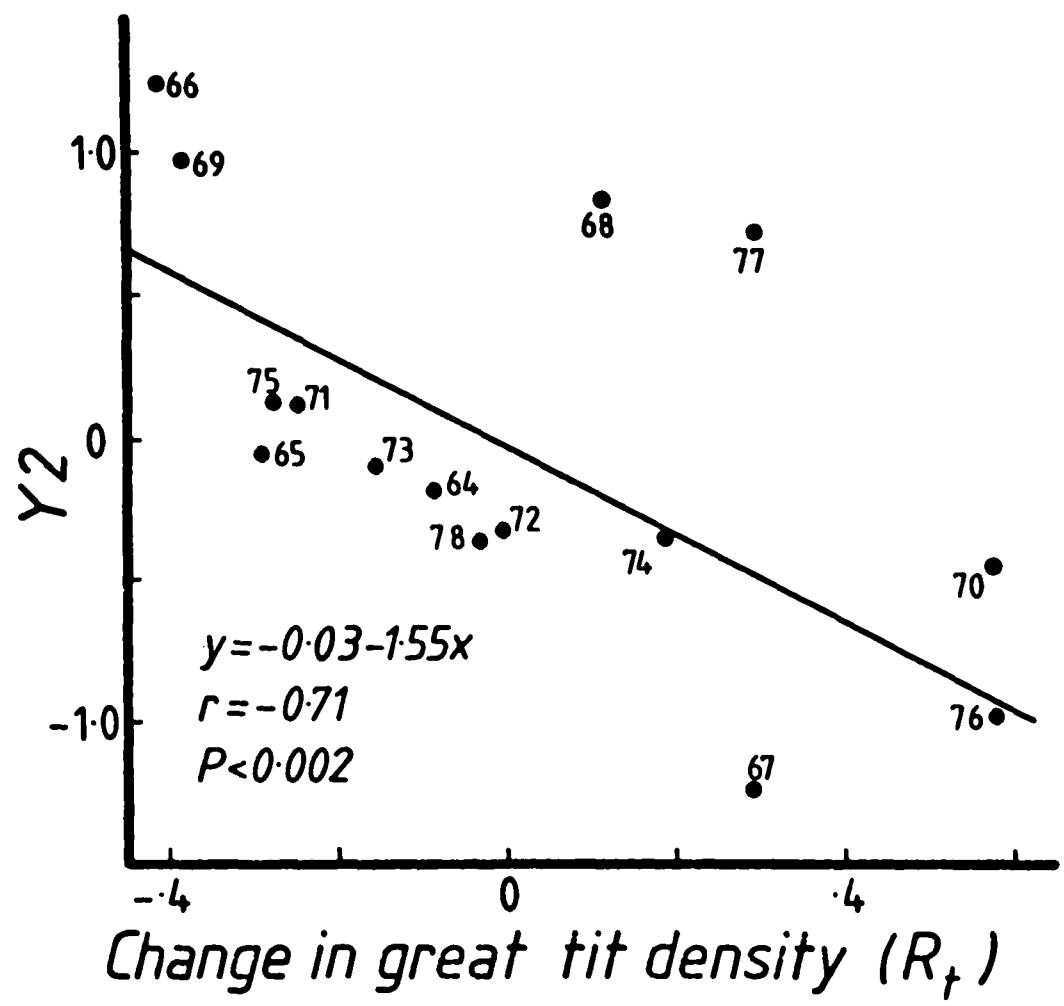
This was not the case as the $\log_e$ ratio of great tits in the two sections was not related to great tit density in the other six sections of Wytham ($r = -0.11$, $n = 16$, n.s.). The simple correlations of the relevant variables are shown in Table 2.14.

An analysis similar to the preceeding one may be done with year to year changes in numbers rather than actual numbers. The dependent variable was an index of blue tit versus great tit change in the two areas

$$Y2 = R_{GT,B} - R_{BT,B} - R_{GT,CP} + R_{BT,CP}$$

where R is the $\log_e$ ratio of the number of breeding birds in one year divided by the number in the preceding year, BT and GT are for blue and great tit, and B and CP are for





Figures 2.7 A&B Effects of great tit breeding density on the relative competitive ability of blue and great tits in Marley Wood and Common Piece. Great tit density as an independent variable was measured in the other six sections of Wytham Woods (MP, E, W, O, C & SW). A) The effect of great tit breeding density on Y1 = $\ln((GT_B/BT_B)/(GT_{CP}/BT_{CP}))$. B) The effect of changes in great tit density (R_t) on Y2 (see text for an explanation of Y2). Great tits did relatively better in Marley Wood as compared with Common Piece as Y1 or Y2 increased.

Table 2.14. Correlation matrix of factors associated with the numbers of blue and great tits in Marley Wood and Common Piece from 1964 to 1979 (n=16, df=14). Data are from or derived from Table 2.3&4. GTB, GTCP, BTB and BTCP are the numbers of blue tits (BT) and great tits (GT) in Marley Wood (B) and Common Piece (CP). GTS and BTS are the sum of great tits and blue tits in the remaining six sections of Wytham. GTBGTCP and BTBBTCP are the log ratios of Marley to Common Piece numbers of great tits and blue tits. GTBBTB and GTCPBTCP are the log ratios of numbers of great tits to blue tits in Marley and Common Piece. Y1 = GTBBTB - GTCPBTCP = GTBGTCP - BTBBTCP. YEAR is a time subscript variable (ie. 1964=1, 1965=2 ... 1979=16).

GTCP	.33										
BTB	.01	.42									
BTCP	-.62	-.18	.39								
GTS	.67	.67	.41	-.28							
BTS	-.44	.19	.78	.82	.01						
GTBTB	.71	-.03	-.65	-.69	.17	-.81					
GTBTCP	.66	.69	-.01	-.82	.62	-.47	.46				
GTBGTCP	.51	-.61	-.30	-.32	-.09	-.47	.60	-.10			
BTBBTCP	.63	.47	.33	-.72	.60	-.27	.19	.83	.09		
Y1	-.20	-.78	-.46	.40	-.56	-.07	.22	-.76	.55	-.78	
YEAR	-.78	-.01	.28	.88	-.26	.74	-.73	-.65	-.62	-.67	.18
	GTB	GTCP	BTB	BTCP	GTS	BTS	GTBTB	GT BTCP	GTB GTCP	BTB BTCP	Y1

Marley Wood and Common Piece. The independent variables were the great tit and blue tit log ratios of breeding numbers in the other six sections of Wytham. If an increase in the number of great tits in the wood resulted in a greater restriction of boxes accessible to blue tits, then an increase in great tits should cause a drop in the index Y2. This was just what happened (Figure 2.7B). The index Y2 was significantly negatively correlated with the change in great tit numbers ($r = -0.71$, $P < 0.002$, $n = 15$), but the correlation between changes in blue tit numbers and Y2 was not significant either as a simple correlation ($r = -0.29$, $P < 0.20$) or as a partial correlation, correcting for the changes in great tit numbers ($t = 0.003$, $df = 12$). A correlation matrix of the relevant variables is in Table 2.15.

The evidence of competition for nest sites has been observational rather than experimental. Other evidence for competition is discussed in Chapter 3 where it is shown that great tits dominate in taking nest boxes in Marley, a section with a high density of nest boxes. In sections with a low density of nest boxes the change in great tit density should have an even greater effect on the number of blue tits breeding in nest boxes. Although blue tits may not occupy many boxes in sections of low box density during years of high great tit density, they could still establish territories and breed in natural sites. Thus, they may compete with great tits for resources other than nest boxes. From this stand point the use of population data from sections with higher nest-box densities may

Table 2.15. Correlation matrix of factors associated with the year to year changes in numbers of blue and great tits in Marley Wood and Common Piece from 1964-1979 (n=15, df=13). Data are derived from Table 2.3&4. Variables are comparable to those in Table 2.14. except that relative changes in number, rather than absolute numbers, are used. RGTB, RGTCP, RBTB and RBTCP are the log ratios of numbers in year n to numbers in year n+1. RGTS and RBTS are the log ratios of changes in the other six sections of Wytham. RGTBTB = RGTB - RBTB; RGTBTCP = RGTCP - RBTCP; RGTBGTCP = RGTB - RGTCP; RBTBBTCP = RBTB - RBTCP; Y2 = RGTBBTB - RGTCPBTCP = RGTBGTCP - RBTBBTCP. YEAR is a time subscript variable (ie. 1964= 1, 1965=2 ... 1979=16).

RGTCP	.83										
RBTB	.75	.68									
RBTCP	.15	-.14	.12								
RGTS	.82	.89	.68	-.18							
RBTS	.70	.51	.86	.46	.47						
RGTBTB	.37	.22	-.34	.04	.21	-.22					
RGTBTCP	.59	.88	.49	-.60	.80	.19	.16				
RGTBGTCP	-.26	-.76	-.30	.41	-.58	-.07	.05	-.82			
RBTBBTCP	.48	.63	.70	-.62	.66	.35	-.30	.82	-.53		
Y2	-.44	-.78	-.61	.61	-.71	-.27	.22	-.93	.82	-.92	
YEAR	-.01	.13	-.05	-.20	.15	-.15	.06	.21	-.23	.10	-.18
	RGTB	RGTCP	RBTB	RBTCP	RGTS	RBTS	RGT BTB	RGT BTCP	RGTB GTCP	RBTB BTCP	Y2

provide less biased estimates of breeding numbers of tits.

Key-factor analyses

It would be helpful to have a simple method of analysing population data that indicated whether two species were competing with each other. One possibility would be to look for a negative correlation between the annual densities of the two species. This is what Hogstad (1975) did with his populations of brambling (Fringilla montifringilla) and willow warbler (Phylloscopus trochilus) in Norway. Hogstad gave other evidence to support his analysis and conclusion of interspecific competition. However, this method can incorrectly indicate competition or fail to detect competition in the event of long term habitat change or large fluctuations in the environment. An example of the former problem may be found in the population data from the Forest of Dean, Gloucestershire (Table 2.16). Blue tit and pied flycatcher (Ficedula hypoleuca) numbers from 1949 to 1977 (data for 1968 missing) were negatively correlated ($r = -0.66$, $P < 0.001$, $n = 28$). However, this correlation might have been caused by long term habitat changes rather than interspecific competition. The correlation between year (either actual calendar year or a time-subscript variable 't' such that for 1949, t=1; 1950, t=2; ...; 1977. t=29) and blue tit numbers was positive ($r = 0.75$, $P < 0.001$) and the correlation between year and pied flycatcher numbers was negative ($r = -0.85$, $P < 0.001$). The partial correlation between blue tit and pied flycatcher numbers, correcting for year, was not significant ($r = -0.08$). It is possible that the increase in blue tits

Table 2.16. Breeding numbers of pied flycatchers, blue tits and great tits in the Forest of Dean. Data from Campbell (1968) and by courtesy of N.C.C. and R.S.P.B.

YEAR	PIED-FLYCATCHER	GREAT TIT	BLUE TIT
1949	67	44	61
1950	87	37	37
1951	100	31	54
1952	98	22	41
1953	85	17	38
1954	76	27	48
1955	67	17	35
1956	60	25	50
1957	54	75	79
1958	71	28	49
1959	71	36	55
1960	58	20	49
1961	62	45	72
1962	59	21	46
1963	58	16	42
1964	57	23	46
1965	64	33	63
1966	70	24	97
1967	63	15	87
1968	-	-	-
1969	49	26	86
1970	50	21	57
1971	54	25	68
1972	55	22	71
1973	44	19	84
1974	33	16	103
1975	35	25	102
1976	36	23	84
1977	38	44	138

meant greater competition for nest sites and that the earlier nesting blue tits were able to maintain possession of their boxes. It might also be that the decrease in pied flycatcher numbers resulted in a competitive release for blue tits or that the population changes of the two species result solely from habitat changes. Additional information might make one of these possibilities the more likely. However, the negative correlation between blue tit and pied flycatcher numbers alone should not be used to infer interspecific competition.

Marley Wood

In Marley Wood there has been no significant correlation between numbers of great and blue tits from 1949 to 1979 ($r = 0.18$, $P < 0.20$). As in the Forest of Dean, and throughout England, there has been an increase in the number of blue tits but not great tits. In Marley Wood the correlation between blue tit numbers and year was high ($r = 0.63$, $P < 0.001$), but between great tit numbers and year the correlation was low ($r = -0.08$, n.s.). Instead of comparing the absolute numbers in the Wood each year, the changes in number from one year to the next may be compared. As a measure of change, I shall use the $\log_e$ ratio of numbers in one year divided by the number in the preceeding year or $R_t = \ln(N_{t+1}/N_t)$ where N_{t+1} is the number of species N in year t+1 and N_t is the number of species N in year t. In Marley Wood there has been a significant correlation between changes in blue tit and great tit numbers ($r = 0.79$, $P < 0.001$). This suggests that annual environmental factors have affected the two species simi-

larly so that the two species tend to fluctuate in parallel even though their absolute densities are not correlated. In Marley Wood the lack of correlation between blue and great tit numbers was largely caused by the increase in the blue tit but not the great tit numbers. Much the same pertains to the blue and great tits in the Forest of Dean. Correlation matrices of relevant variables for both locations are in Table 2.17.

The correlation between blue and great tit changes in breeding density suggests that the two species react similarly to environmental changes. Perrins (1966) and Webber (1975) showed that changes in the great tit breeding populations in Wytham and Holland were closely related to the beech mast crop in the intervening autumn. Slagsvold (1975) showed that March temperatures were correlated with the breeding numbers of blue and great tits in Wytham from 1947 to 1964. Webber (1975) pointed out that high March temperatures and good beech mast crops happened to be correlated between 1947 and 1964. He found that great tit numbers were not related to March temperatures from 1965 to 1974. Further, he found that for all years, 1947 to 1974, the partial correlation between great tit numbers and March temperatures, correcting for an index of the beech mast crop, was not significant. Nevertheless, Webber thought that spring temperatures might affect the numbers of blue tits. Van Balen (1978) has also suggested that great tit numbers in Holland are related to the abundance of beech mast but not winter severity.

Data from Broder Bejer (pers. comm.) shows that great

Table 2.17. Correlation matrices for breeding birds in Marley Wood (1949-1979) and the Forest of Dean (1949-1979 less 1968). RGT, RBT and RPF are the log ratios of number in one year to the number in the preceeding year for great tits, blue tits and pied flycatchers. GT, BT and PF are the numbers of great tits, blue tits and pied flycatchers. YEAR is a time subscript variable.

Marley Wood (d.f.=28)

GT	.01			
BT	.67	.18		
RGT	.10	-.48	-.42	
RBT	-.02	-.33	-.46	.79
	YEAR	GT	BT	RGT

Forest of Dean (d.f.=24)

GT	-.33					
BT	.72	.12				
PF	-.84	.11	-.66			
RGT	.12	-.63	-.23	.07		
RBT	.17	-.53	-.31	-.10	.72	
RPF	-.12	.52	.06	-.16	-.02	-.16
	YEAR	GT	BT	PF	RGT	RBT

tit breeding numbers in Denmark are highly correlated with the abundance of winter foods. Spruce seeds, beech mast and aphid abundance were all significant factors affecting breeding numbers. Winter temperatures were not a significant factor except in the absence of aphid abundance from the regression model. There was a high correlation between aphid abundance and winter temperatures. The inference is that cold winters per se do not affect great tit numbers, but they may affect the abundance of insect foods. It may also be that ice or snow storms affect the accessibility of food items.

In addition to environmental variables such as weather and the food supply, changes in the breeding numbers may be affected by the numbers of birds breeding in the previous year. This may be both the number of conspecifics as well as interspecific competitors.

I used a key-factor model to test whether the changes in the breeding densities of blue tits and great tits were related to the densities of blue tits, great tits, winter food and winter weather. Winter food was represented by a dummy variable (B_t) for good and bad beech mast crops. Winter weather was measured as the mean low temperature for March (T_{t+1}). The numbers of blue and great tits were their $\log_e$ densities. Thus, the regression model was

$$P_{t+1} - P_t = a_0 + a_1 P_t + a_2 Q_t + a_3 T_{t+1} + a_4 B_t$$

where a_0 is the regression constant, $a_1 - a_4$ are the regression coefficients, and P_t and Q_t are the $\log_e$ densities of blue and great tits (or vice versa) in year t. Note

that the expression ($P_{t+1} - P_t$) is the same as R_t defined above.

The regression model was fitted in steps. The log density of species P was fitted in the first step. In the second and subsequent steps the remaining variate that most reduced the error mean square of the regression was added to the model.

The results of the analysis (Table 2.18) show that changes in great tit density have been related to blue tit and great tit densities and the beech mast crop. Changes in blue tit density have not been related to great tit density but to blue tit density, March temperatures and the beech mast crop. The addition of March temperatures to the model for great tit change was only significant with 90 percent confidence. An index of winter severity, other than the March temperatures suggested by Slagsvold (1975), might be more significant.

The results for the two species are in accord with their winter ecology. Great tits are nearly twice the weight of blue tits and might be less affected by cold. Also, from January to April blue tits forage mostly in the branches of trees while great tits forage mostly on the ground. By January almost all beech mast has fallen to the ground. Although both species use beech mast, it is more important in the diet of great tits. Blue tits are more likely to feed on insects and insect abundance is affected by temperature.

In addition to the factors affecting overwintering survival, the key-factor analysis suggests that at some

Table 2.18. Regression model for factors affecting changes in great tits in Marley Wood from 1949 to 1979. GT and BT are the log densities of great tits and blue tits (pairs per hectare). MMLF is the mean March low temperature (°C). MAST is the dummy variable for beech mast abundance (1=good crop, 0=poor crop). Independent variables are listed in order of their inclusion in the model. The t-test for each variable is a measure of the significance of each estimated coefficient. '%V' is the increase in percentage variance explained by adding each variable to the model. Except for the constant, probabilities are one-tailed. The model for great tits is given both with and without MMLF.

Change in Density of Blue Tits (42.5% of variance explained)

	Coefficient	t	$P_t <$	% V	$P_V <$
Constant	-.234	1.95	0.05		
BT (P_t)	-.332	2.62	0.01	17.1	0.01
MMLF (T_{t+1})	.0914	2.04	0.05	19.2	0.005
MAST (B_t)	.324	1.98	0.05	6.2	0.05

(addition of GT would increase residual mean square)

Change in Density of Great Tits (58.9% of variance explained)

	Coefficient	t	$P_t <$	% V	$P_V <$
Constant	-0.0184	.27	n.s.		
GT (P_t)	-0.275	1.87	0.05	24.4	0.002
MAST (B_t)	0.531	4.35	0.001	28.0	0.001
BT (Q_t)	-0.236	2.30	0.02	6.5	0.02

Change in Density of Great Tits (61.3% of variance explained)

	Coefficient	t	$P_t <$	% V	$P_V <$
Constant	-0.151	1.44	0.25		
GT (P_t)	-0.235	1.62	0.10	24.4	0.002
MAST (B_t)	-0.451	3.52	0.001	28.0	0.001
BT (Q_t)	-0.241	2.42	0.02	6.5	0.02
MMLF (T_{t+1})	0.0559	1.62	0.10	2.4	0.10

point during the year blue tits adversely affected the great tit population and that the effect was density dependent (see also Dhondt 1977, Minot 1978, Dhondt 1978). This method of analysis does not indicate when competition occurs during the year. In Chapter 6 I show that great tit breeding success at fledging is related to blue tit breeding density.

Ghent, Belgium

Marley Wood is but one place where blue and great tits breed. To check that the results for Marley Wood apply to other localities, I did similar key-factor analyses on population data from other studies. André Dhondt (1977) published population data on blue and great tit numbers in Belgium. The data used to produce his Figure 3 are given in Table 2.19. As in Marley Wood the nest boxes in Ghent were well in excess of breeding numbers, with about 7 boxes per hectare. Also, as in Marley there was a low correlation between the numbers of blue and great tits in each year ($r = 0.20$). The correlation between changes in blue tit and great tit numbers was higher ($r = 0.43$, $n = 16$, $P < 0.05$, one-tailed). In Table 2.20 I show the results of a key-factor analysis of Dhondt's data using a regression model similar to that used for Marley Wood. I again used the Dutch beech mast data, but included no winter temperatures except a dummy variable for the hard winter of 1963.

The results of the analysis are in essential agreement with the results for Wytham and support Dhondt's (1977) more qualitative conclusion that changes in the

Table 2.19. Breeding density (pairs per hectare) of blue and great tits at Ghent, Belgium. Data from Dhondt (1977). 'Beech Crop' is a dummy variable derived from the Dutch beech mast index (1=good crop, 0=poor crop).

YEAR	GREAT TIT	BLUE TIT	BEECH CROP
1960	0.96	1.09	1
1961	1.74	1.17	0
1962	1.30	1.09	0
1963	1.04	0.65	0
1964	1.77	0.81	0
1965	2.04	1.00	0
1966	1.58	1.00	0
1967	1.62	1.19	0
1968	1.77	1.15	0
1969	1.69	1.00	0
1970	1.69	1.12	1
1971	2.38	0.92	0
1972	2.04	0.96	0
1973	1.58	1.27	0
1974	1.46	0.88	1
1975	2.04	1.08	0
1976	1.27	0.73	1

Table 2.20. Effects of blue and great tit density, beech crop and a severe winter on the change in breeding numbers of blue and great tits at Ghent, Belgium. BT and GT are the log densities of blue and great tits in pairs per 10 hectares. MAST is a dummy variable for the beech mast crop. W is a dummy variable for the cold winter of 1963.

Change in Blue Tit Density (58.4% of variance explained)

	Coefficient	t-test	$P_t <$	% V	$P_V <$
Constant	1.98	3.53	0.005		
BT (Q_t)	-0.853	3.52	0.002	37.8	0.005
W (T_{t+1})	-0.456	2.82	0.01	20.6	0.01

Change in Great Tit Density (80.5% of variance explained)

	Coefficient	t-test	$P_t <$	% V	$P_V <$
Constant	3.21	5.32	0.001		
GT (P_t)	-0.769	4.33	0.001	51.6	0.001
W (T_{t+1})	-0.345	2.25	0.025	15.3	0.01
MAST (B_t)	0.292	2.91	0.01	7.9	0.025
BT (Q_t)	-0.470	2.12	0.05	5.7	0.05

great tit population were affected by blue tit numbers, but that changes in the number of blue tits were independent of great tit numbers. The effect of the beech mast crop was not as great as in Wytham, but the beech crop did have a significant effect on changes in the numbers of great tits. The inclusion of a dummy variable for 1963 was based on Dhondt's a postiori estimation of its importance. The dummy variable was statistically significant but a single hard winter cannot be used to establish a causal relationship.

Forest of Dean

Nest boxes in the Forest of Dean have been principally used by pied flycatchers, blue tits and great tits. Nuthatches (Sitta europa), redstarts (Phoenicurius phoenicurius), coal tits (Parus ater) and marsh tits (Parus palustris) also breed in boxes but never in large numbers. The density of nest boxes has been about 10.5 per hectare (ca 250 boxes on 24 ha). This included 40-60 trees with two boxes each. Both boxes of a pair were not used very often, so that the effective density may have been 8-9 boxes per hectare. The percentage of boxes occupied varied from 50 to 95 percent. General descriptions of the Forest of Dean and the nest-box scheme are in Lack (1966) and Campbell (1968). I have already given the breeding numbers in Table 2.16, and noted the long term trend toward more blue tits and fewer pied flycatchers. In the key-factor analysis of these populations I included a time subscript variable YEAR which was equal to 't' (where for 1949, t=1; 1950, t=2; etc.) to account for long term

shifts in the equilibrium of the populations. As before the beech crop was included as a dummy variable based on the Dutch beech mast index. Winter temperatures were not included in the model. Thus, the model was a slight modification of that used for Wytham and Ghent, namely

$$P_{t+1} - P_t = a_0 + a_1 P_t + a_2 Q_t + a_3 S_t + a_4 B_i + a_5 YEAR$$

where P_t, Q_t and S_t are the log numbers of the three species in year t, YEAR = t, B is a dummy variable for the beech crop, a_1 to a_5 are the regression coefficients and a_0 is the regression constant. As before the intraspecific numbers were fitted first and then, successively, the term that most reduced the error mean square for the regression. The analyses for the three species are in Table 2.21. Note that because of the missing data for 1968, each analysis is based on 26 samples coming from 28 years of data.

The interpretation of the results is made more difficult by the presence of pied flycatchers. The positive correlation between changes in pied-flycatcher numbers and the number of great tits is confusing. The most likely explanation is that pied-flycatcher numbers were depressed in years when the numbers of great tits were high. The correlation between great tit and pied flycatcher numbers was negative ($r = -0.71$, $n = 28$, $P < 0.001$). The partial correlation between great tit and pied flycatcher numbers, correcting for the time-subscript variable YEAR, was also negative, but much less significant ($t = 1.75$, $P < 0.05$, one-tailed). Because the numbers of great tits see-sawed as a result of changes in factors such as the beech crop, pied

Table 2.21. Factors affecting the change in breeding numbers of pied flycatchers, great tits and blue tits in the Forest of Dean. PF, GT and BT are log numbers of pied flycatchers, great tits and blue tits.

Change in Pied Flycatcher Numbers (33.2% of variance explained)

	Coefficient	t-test	$P_t <$	% V	$P_V <$
Constant	1.28	1.66	0.20		
PF	-0.400	2.61	0.01	-1.6	n.s.
GT	0.156	2.32	0.02	25.4	0.005
YEAR	-0.0112	2.06	0.05	9.4	0.05

Change in Great Tit Numbers (72.2% of variance explained)

	Coefficient	t-test	$P_t <$	% V	$P_V <$
Constant	3.38	4.49	0.001		
GT	-0.644	4.21	0.001	40.6	0.001
MAST	0.659	5.21	0.001	27.0	0.001
BT	-0.360	2.20	0.02	4.6	0.02

Change in Blue Tit Numbers (52.9% of variance explained)

	Coefficient	t-test	$P_t <$	% V	$P_V <$
Constant	3.13	4.44	0.001		
BT	-0.870	4.58	0.001	7.8	0.05
YEAR	0.0277	3.69	0.001	35.6	0.001
MAST	0.244	2.38	0.02	9.1	0.02

flycatchers could increase in numbers in the year following a high population of great tits. Further, the migratory pied flycatchers were in competition with tits only during the breeding season. Flycatchers bred two to three weeks later than the blue and great tits (Campbell 1968). They fed their young after the period of caterpillar abundance (Lack 1966:98). Hence, pied flycatcher numbers were probably limited by the availability of nest boxes. Competition for food between flycatchers and tits was probably much lower than between blue and great tits.

Changes in blue and great tit numbers were not related to the breeding numbers of pied flycatchers. This is probably because the flycatchers bred later than the tits in boxes that would not have been occupied by tits and because there was little intergeneric competition for food. The regression results for blue and great tits are similar to those for blue and great tits in Wytham Woods and at Ghent. Both blue and great tits increased in years following a good beech crop. Also, the great tit population tended to decrease in years following a high population of blue tits. As in Marley Wood, there was a low correlation between the numbers of blue and great tits ($r = 0.20$, $n = 28$, $P < 0.20$), but a high correlation between the annual changes in the two populations ($r = 0.72$, $n = 26$, $P < 0.001$).

Wageningen, Holland

The analysis of the three tit populations (Marley Wood, Ghent, and Forest of Dean) have not examined independent events. Beech mast, winter temperatures and tit

populations are correlated over large areas. Data from an early nest-box study at Oranje Nassau's Oord (ONO) near Wageningen, Holland (Kluijver 1951) provide a check on the results from Marley Wood, Ghent, and the Forest of Dean. The population data come from Kluijver's Table 48 and data on winter cold from his Figure 10. I counted as cold winters those with a 'cold figure' of greater than 70. Years of good beech mast were determined, as before, from the Dutch beech mast index for 1930 to 1942. For years prior to 1930 I used data from the British Forestry Commission. I counted as good years those with a quantity of beech mast described by the Commission as 'moderate' or better. The data I used are in Table 2.22.

The nest boxes at ONO were at a density of 2.3 to 2.9 per hectare (300 - 380 boxes in 129 hectares). Despite the low density of boxes, occupation varied from 10 to 40 percent so that a surplus of boxes existed in all years. Kluijver thought that most breeding blue and great tits used nest boxes, but that crested tits (Parus cristatus) and coal tits were more likely to use natural sites.

With such a low breeding density and so many congeners breeding in the same area, the pattern of competition might be different from that in Marley Wood, Ghent and the Forest of Dean. However, the effect of winter severity and winter food might be similar. This was generally true (Table 2.23). Good beech mast crops were correlated with increases in the great tit population and possibly with the blue tit population as well. Hard winters were followed by a drop in the blue tit population. The effect of congeners was not

Table 2.22. Breeding numbers of tits in boxes at Oranje Nassau's Oord, Holland. COLD is a dummy variable for winter temperature (1=cold, 0=warm). MAST is a dummy variable for beech mast abundance (1= good crop, 0=poor crop).

YEAR	COLD	MAST	GREAT TIT	BLUE TIT	COAL TIT	CRESTED TIT
1912	-	1	22	5	7	6
1913	0	0	40	6	7	7
1914	0	0	41	9	22	8
1915	0	1	30	8	8	5
1916	0	0	63	11	10	7
1917	1	1	19	2	8	3
1918	0	0	40	7	10	5
1919	0	0	67	15	11	12
1920	0	1	28	12	12	12
1921	0	0	34	10	7	6
1922	1	1	30	2	5	5
1923	0	0	39	8	7	9
1924	1	1	28	6	1	6
1925	0	0	92	22	8	10
1926	1	1	41	17	9	5
1927	0	0	63	15	11	3
1928	1	0	49	15	19	3
1929	1	1	48	12	13	3
1930	0	0	72	20	12	2
1931	0	0	65	11	7	1
1932	0	0	57	12	10	1
1933	1	1	59	18	11	5
1934	1	0	85	21	14	3
1935	0	1	55	21	14	5
1936	0	0	78	24	20	4
1937	0	0	82	21	13	6
1938	0	0	76	26	13	3
1939	1	0	44	22	7	3
1940	1	1	45	11	4	3
1941	1	0	93	13	4	5
1942	1	1	18	15	5	1
1943	0	0	76	11	8	4

Table 2.23. Factors affecting the change in breeding numbers of great tits and blue tits at Oranje Nassau's Oord, Holland. GT, BT and Ct are log numbers of great, blue and crested tits. MAST is a dummy variable for beech mast (1=goodcrop, 0=poor crop). COLD is a dummy variable for winter temperature (1=cold, 0=mild).

Change in Great Tit Numbers (70.2% of variance explained)

	Coefficient	t-test	$P_t <$	% V	$P_V <$
Constant	2.90	3.65	0.001		
GT	-0.686	3.59	0.001	51.9	0.001
MAST	0.563	3.27	0.002	9.9	0.005
CT	-0.294	2.93	0.005	8.4	0.005

Change in Blue Tit Numbers (35.9% of variance explained)

	Coefficient	t-test	$P_t <$	% V	$P_V <$
Constant	1.45	3.56	0.001		
BT	-0.507	3.08	0.005	28.3	0.001
COLD	-0.435	2.07	0.025	7.6	0.025

Change in Blue Tit Numbers (47.8% of variance explained)

	Coefficient	t-test	$P_t <$	% V	$P_V <$
Constant	-1.38	1.23	n.s.		
BT	-0.725	3.73	0.001	28.3	0.001
COLD	-0.371	1.88	0.05	7.6	0.025
MAST	0.627	2.58	0.01	2.2	0.10
GT	0.802	2.42	0.02	9.7	0.02

as clear as in the other three studies. At ONO great tits were apparently affected by coal tits much as they were affected by blue tits in the other study areas. If coal tit numbers were indeed much greater than the number breeding in nest boxes and if the number breeding in nest boxes was in proportion to the true breeding population, then this result makes some sense. However, it is still surprising that the apparently more numerous blue tits had no significant effect on changes in the great tit population. The results for blue tits are also complicated. If the step-up regression procedure is stopped before the first non-significant term is added, then only winter temperatures and blue tit numbers are included. However, the addition of <u>both</u> beech mast and the number of great tits results in a significant increase in the amount of variance explained. The number of great tits in the previous year is positively correlated with the change in blue tit numbers. There are several possible explanations for this. First, as suggested for the pied flycatchers in the Forest of Dean, the blue tits may experience a competitive release following a peak in the 'see-sawing' great tit population. Second, there are strong correlations between the numbers of blue tits and great tits ($r = 0.66$) and between great tit numbers and the beech crop in the same year ($r = -0.62$). Thus, the relationship between the number of great tits and changes in the numbers of blue tits may not be causal.

The analysis of Kluijver's data does not provide a wholly satisfactory confirmation of the results from Marley

Wood, Ghent, and the Forest of Dean. The effects of winter cold and beech mast are confirmed, but the effects of blue and great tits on each other are not at all clear. The low breeding densities, coniferous woods with a few mixed-deciduous species, and the presence of four congeners must have created a much different environment for competition.

CONCLUSIONS

Comparisons amongst the eight sections of Wytham Wood and sixteen years of breeding data provided strong support for the view that the great tit was the better interference competitor when it came to securing a nest box for breeding. The evidence for this was presented in several ways. Blue tit numbers were more affected by nest-box density than were great tit numbers. I showed that changes in blue tit and great tit numbers were more positively correlated at high nest-box densities. The variance in blue tit, but not great tit, numbers decreased in years of low great tit density or in sections with high densities of nest boxes. Finally, comparisons between sections with high and low densities of nest boxes showed that when the number of great tits increased, blue tit numbers were relatively higher in the section of high nest-box density.

Great tits may be the better interference competitors, but they seem to lose at scramble competition. The key-factor analyses of three populations breeding at high densities showed that changes in the density of great tits were negatively related to the density of blue tits but not vice versa. This result suggests that a Lotka-Volterra

graph for blue and great tits may look like Figure 2.8, as previously suggested by Dhondt (1977). The analyses do not reveal how the blue tit might gain an edge in scramble competition. This is discussed in the following chapters.

Despite the similar resource requirements of the two species, the abundance of beech mast and the severity of winters affected the two species differently.On the whole, blue tits were more sensitive to cold winters and great tits to changes in the beech crop. In the remaining chapters I shall concentrate on competition during the breeding season and look further at the resource requirements of the two species at that time.

The picture of the blue tit as the better scramble competitor and the great tit as the better interference competitor will be reinforced in most respects. The idea that the largest species of a guild is the best interference competitor is not new. Ford (1979) made just such an observation for the Australian nectar-feeding honeyeaters (Meliphagidae), finding that the largest species dominated the richest food patches, while the smaller species could maintain themselves on the poorer patches.

The compulsion for ecologists to divide species according to r - vs K-selected has happily waned. Blue and great tits are not clearly divisible along these lines. Nevertheless, in reading the remaining chapters, it may be useful to try fitting the great tit into the role of the K-selected species and to consider the blue tit as r-selected. Blue tits certainly move over greater distances,

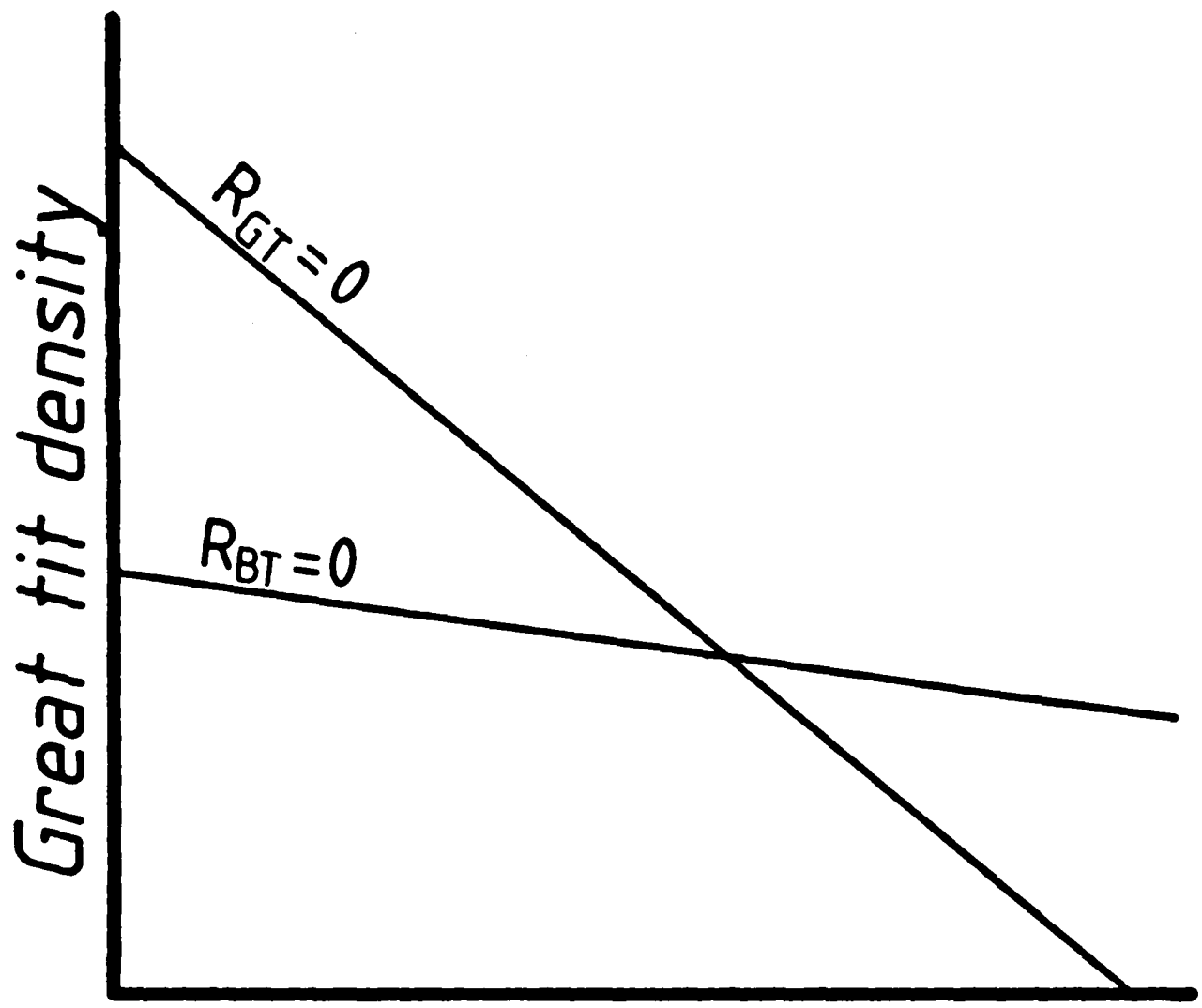


Figure 2.8 Lotka-Volterra graph of blue tit and great tit competition based on annual breeding densities.

have larger clutches and higher annual adult mortality and are good scramble competitors. If the division fails in other respects, it will have at least invited critical comparisons.

CHAPTER 3

Territoriality and Nest Site Selection

If different species compete for the same resources during the nesting season then one might expect there to be some form of interspecific territoriality. Such behaviour would benefit the individual territory holders of at least one of the species by providing an area exclusive of competitors. Conversely, the existence of interspecific territories could be taken to suggest strong evidence for competition between two species. However, the absence of interspecific territoriality would not necessarily imply an absence of competition between the two species.

Even if there were no interspecific territories it is possible that two species might space their nests out so that neighbouring pairs of different species are as far apart as possible. Such spacing would imply that there was resource competition between the two species, but it would always be possible that the spacing had arisen for other reasons such as the avoidance of predators or habitat segregation.

Finally, competition may not be organized by any form of interspecific spacing. All competition may be directly for the resources that are required. This could include competition for nest sites which may be limited and similar for the two species. If there is competition for nest sites then there should be a number of nest sites which are preferred by, or at least suitable to, both species. One species may be better than the other at competing for these

nest sites. In this case the density of the dominant species may affect the nest site selection of the weaker species.

This chapter examines the territorial behaviour of great and blue tits, the inter- and intraspecific spacing of nest sites, and the selection of, and competition for, nest sites.

METHODS

Mapping territories

Blue and great tit territories were mapped in Higgins' Copse in 1977 and in Marley Wood in 1978. Beginning in early March the tits were trapped in mist nets baited with suet and peanuts. Virtually all great and blue tits later found breeding were trapped. For both species and years approximately two-thirds of the birds ringed eventually settled in a territory and at least constructed a nest. All tits were colour-ringed so that individuals could be recognized at a distance. Ten-power binoculars were sufficient to identify colour rings on great tits. I found a 20-power spotting scope mounted on a gun stock to be better for blue tits and this was used for most work.

In both 1977 and 1978 territories were mapped mostly during April. In the 5.5-hectare Higgins' Copse mapping was based on a 35-m grid plus the positions of the 35 nest boxes. In the 27-hectare Marley Wood I used a 50-m grid and the positions of the 214 nest boxes. Territory mapping in Marley Wood was restricted to the southern part of the wood. All sightings of birds were plotted on a grid map of the area that included box positions. I also noted

whether the bird was singing, feeding or chasing an intruder.

Random use of nest boxes

The predicted distribution of random use of nest boxes over a number of years was calculated by using a trinomial expansion. In each year the probability that a box would be occupied at random by species A is $P(A_i) = a_i/N$ where a_i is the number of breeding pairs of species A in the ith year and N is the constant number of boxes available in the wood over the duration of the study. Similarly, $P(B_i) = b_i/N$ is the probability that each box will be occupied by a pair of species B and $P(U_i) = 1 - P(A_i) - P(B_i)$ is the probability that each box would be unoccupied in the ith year. In each year there will be only one of three possible outcomes at each box, each with an associated probability given random occupancy. By adding a second year there will be six possible unordered outcomes for each box. The predicted distribution of use, assuming random occupancy, depends on the number of pairs of each species in each year. The probability of occupation twice by species A is $P(A_1)\ P(A_2)$, once by species A is $P(A_1)\ P(U_2) + P(U_1)\ P(A_2)$, once by both species $P(A_1)\ P(B_2) + P(B_1)\ P(A_2)$, etc. This expansion may continue over a number of years so that for n years there will be $(n+1) + n + (n-1) + \cdots\cdots\cdots + 1$ possible outcomes. A simple computer program greatly simplified the calculation. The program is shown in Table 3.1.

Table 3.1 SPITBOL program used to compute a trinomial expansion.

```
MACRO SPITBOL VERSION 3.5(14) G3/4 LEEDS UNIV. COPY  003
RUN 23/04/80 AT 15.27

PAGE 1

      * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * *
      *
      * THIS PROGRAM MAKES A TRINOMIAL EXPANSION.  IT IS DESIGNED TO COMPUTE
      * THE EXPECTED DISTRIBUTION OF USE OF M1 BOXES OVER Y YEARS BY TWO
      * SPECIES OF BIRDS ASSUMING RANDOM CHOICE OF BOXES BY THE NUMBER OF
      * BIRDS BREEDING EACH YEAR.                                  E.O. MINOT
      *
      * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * *
1
      -PRINT
      -INCLUDE
2           &ANCHOR = &DUMP = 1
      *
      * DATA INPUT IN-LINE AS A STRING (D) CONSISTING OF NUMBER OF YEARS,
      * NUMBER OF BOXES(CONSTANT), AND NUMBER OF SPECIES 1 & 2 IN PAIRS
      * BY YEAR.  DATA SEPARATED BY COMMAS.  NOTE TERMINAL COMMA ON DATA.
      *
3           D = "14,134,37,31,38,14,33,15,45,17,42,16,50,23,41,18,41,14,"
4           D = D "58,23,51,28,59,15,68,28,48,26,35,19,"
5           D BREAK(',') . N1 ',' BREAK(',') . M1 REM . D
6           J = 0
7           N = N1 + 1
8           M1 = CONVERT(M1,'REAL')
9           NN = N ',' N
10          A1 = 1,0
11          A = ARRAY(NN,A1)
12          SP1 = ARRAY(N)
13          SP2 = ARRAY(N)
14          SP12 = ARRAY(N)  :(L180)
      *
      * AFTER THE 1ST AND SUBSEQUENT YEARS ARRAY B OF USE FOR YEAR J IS
      * TRANSFERRED TO A.  B IS THEN USED FOR CONSTRUCTING THE EXPECTED
      * DISTRIBUTION FOR THE FOLLOWING YEAR (J + 1)
      *
15    L140  A = B
16    L180  J = LT(J,(N - 1)) J + 1  :F(L340)
17          B = ARRAY(NN)
      *
      * FOR YEAR J ASSIGN NUMBER OF SPECIES 1 & 2 TO X & Y AND CALCULATE
      * PROBABILITY OF A BOX BEING TAKEN BY EACH SPECIES
      *
18          D ',' BREAK(',') $ X ',' BREAK(',') $ Y  REM . D
19          X = X / M1
20          Y = Y / M1
21          Z = 1 - X - Y
22    L250  K = 0
23    L251  K = LT(K,J) K + 1  :F(L140)
24          K1 = K + 1
25          L = 0
26    L270  L = LT(L,(J - K + 1)) L + 1  :F(L251)
27          L1 = L + 1

PAGE 2

28          B<K,L> = B<K,L> * Z + A<K,L>
29          B<K,L1> = B<K,L1> + Y * A<K,L>
30          B<K1,L> = B<K1,L> + X * A<K,L>  :(L270)
      *
      * OUTPUT EXPECTED FREQUENCY AND NUMBER OF USES FOR BOTH SPECIES AND
      * CALCULATE SUMMED EXPECTED USE FOR SPECIES 1, SPECIES 2, AND
      * THE TWO SPECIES COMBINED
      *
31    L340  EJECT()
32          OUTPUT =
33          OUTPUT =
34          OUTPUT = "SPECIES1  SPECIES2  FREQUENCY      EXPECTED"
35          OUTPUT =
36    L410  M = LT(M,N) M + 1  :F(EJE)
37          OUTPUT =
38          I = 0
39    L430  I = LT(I,M) I + 1  :F(L410)
40          MM = M - I + 1
41          Z = RPAD(A<MM,I>,15)
42          Z1 = Z * M1
43          SP12<M> = SP12<M> + A<MM,I> * M1
44          SP2<MM> = SP2<MM> + A<I,MM> * M1
45          SP1<MM> = SP1<MM> + A<MM,I> * M1
46          Z1 LEN(15) . Z1
47          OUTPUT = RPAD((M - 1),10) RPAD((I - 1),10)  '  '  Z  Z1  :(L430)
      *
      * OUTPUT SUMMED EXPECTED USE
      *
48    EJE   EJECT()
49          OUTPUT =
50          OUTPUT =
51          I = 0
52          OUTPUT = "USES  SPECIES1     SPECIES2     SPECIES 1 & 2"
53    L500  I = LT(I,N) I + 1  :F(EJE2)
54          OUTPUT = '  ' RPAD((I - 1),7) RPAD(SP1<I>,13) RPAD(SP2<I>,13)
                     RPAD(SP12<I>,13)  :(L500)
      *
55    EJE2  EJECT()
56    END


STORE USED      1854
STORE LEFT      21778
COMP ERRORS     0
REGENERATIONS   0
COMP TIME-MSEC  242
```

RESULTS AND DISCUSSION

Blue and great tit territories

Blue and great tits could reduce possible competition during the nesting season by establishing interspecific territories during the spring. Interspecific territories should insure that the nest sites of both conspecifics and congeners were spaced out. Thus the two species would be engaged in interspecific interference competition in expectation of reduced scramble competition later in the year. Such a system might operate either to the mutual benefit of both species or perhaps primarily to the benefit of the dominant species. For example, great tits might force blue tits into the interstices between great tit territories.

The problem with interspecific territories is in making them work. If the defended resource is plentiful then the cost of defense may not be rewarded. Some sympatric congeners maintain exclusive territories (Orians and Willson 1964) and others do not (Cody 1974). The benefits of interspecific territoriality will change with the overlap between the two species and the nature of the resources that the species use in common. There is no *a priori* expectation for blue and great tits.

The results of great and blue tit territory mapping in Higgins' Copse are shown in Figures 3.1A and 3.1B. In general the territories were clearly defined by aggression at the boundaries between two neighbouring males, usually by two birds singing at each other. The exact boundaries tended to shift with time. The figures show the situation

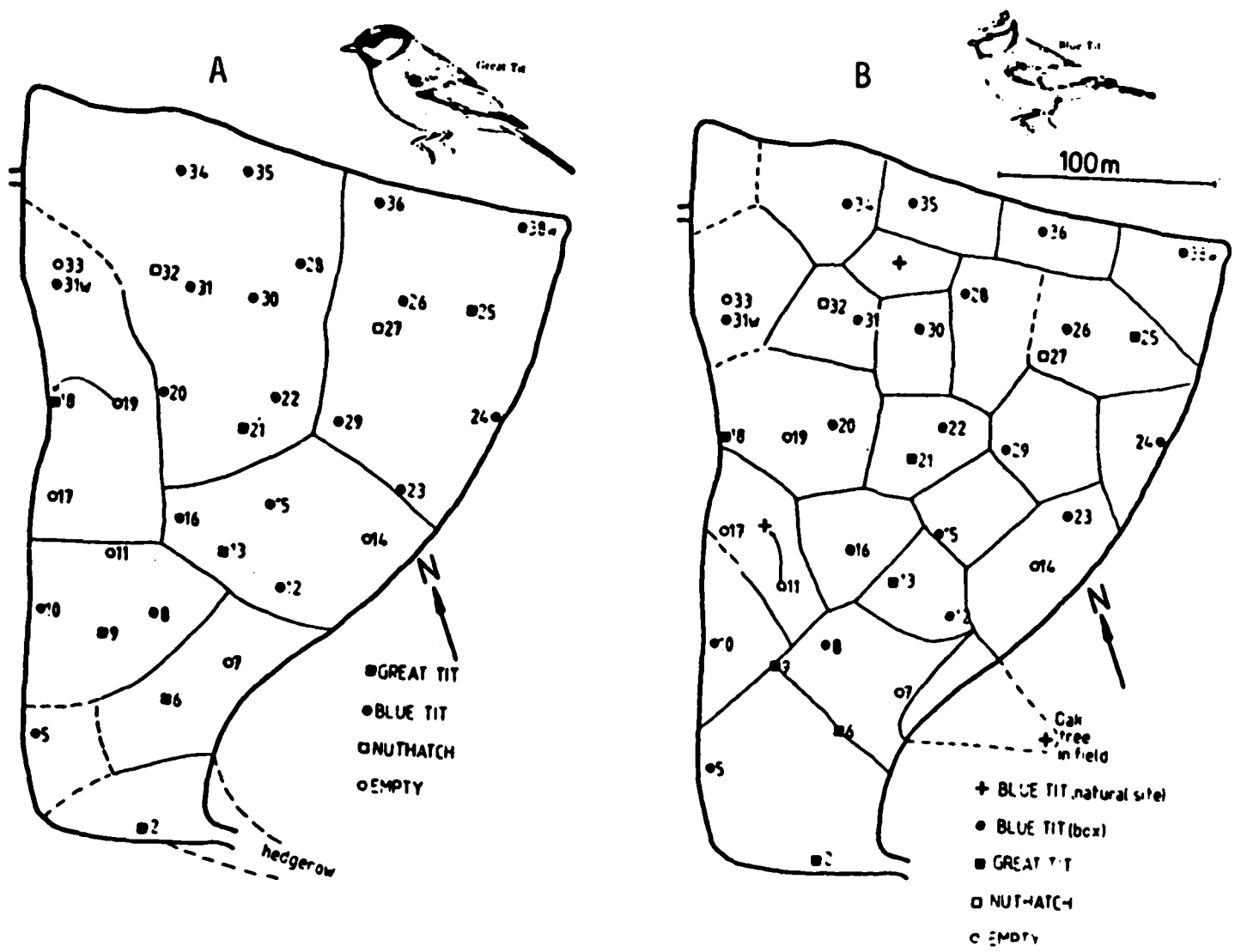
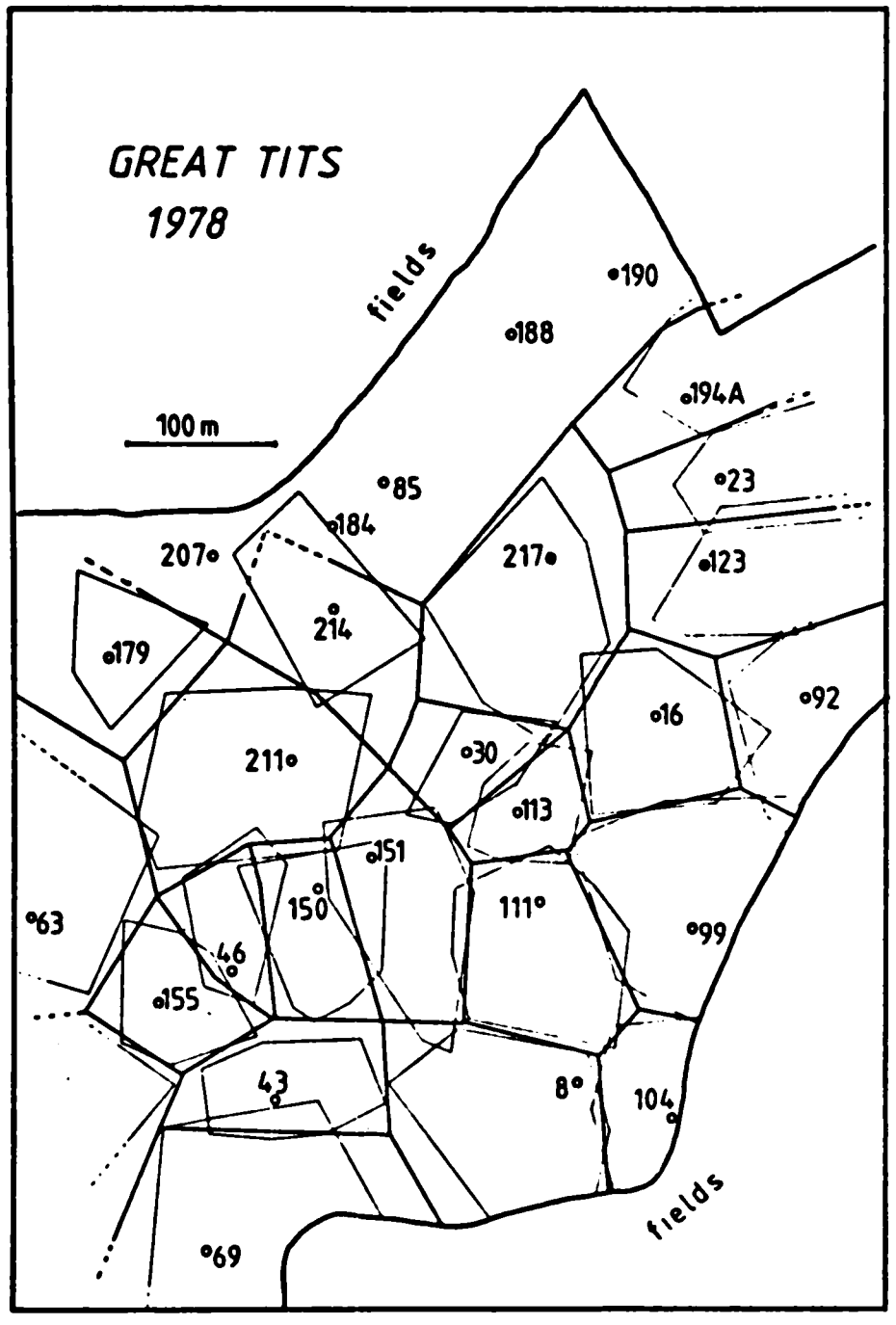


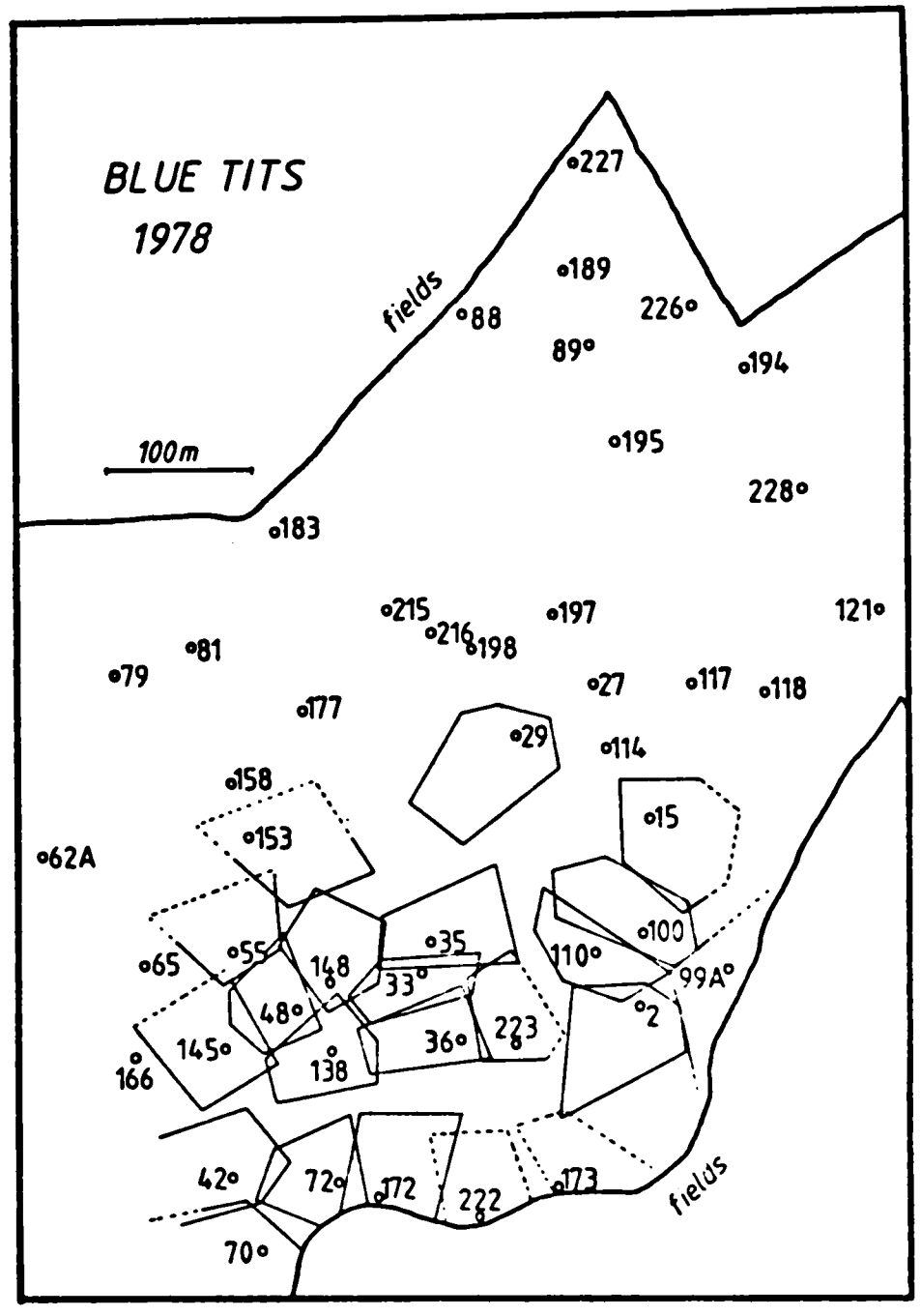
Figure 3.1 Great tit (A) and blue tit (B) territories in Higgins' Copse in mid-April 1977. Solid lines show defended boundaries. Dashed lines show the presumed extent of the territory where no defense was observed. Two pairs changed nest site after starting nest construction, a great tit moved from 19 to 18 and a blue tit moved from 11 to a natural site.

at the end of April, once most nest sites had been established. One reason for the ease of determining boundaries was that both species were nesting at a fairly high density (1.3 great tit pairs / ha, 4.0 blue tit pairs/ ha). Also, all great tits and two-thirds of the blue tits had part of their territory on the edge of the copse.

Despite the high densities there were undefended regions of the copse. Neither species sang in the northwest corner though this space was occasionally used for feeding by birds from the hedgerow west of this corner. The southern end of the copse was almost entirely dead elm trees with an understory of nettles. The blue tit territory here was almost twice the size of any other blue tit territory. This southern area was invaded late in the season, about 10 April, by a great tit pair from the hedgerow southeast of the copse. This pair met little apparent resistance from the previous holder of this area. A space around nest-box 5 was not used at all by great tits. Thus, with the exception of two apparently unsuitable habitats both species formed a mosaic of intraspecifically defended territories over the copse.

The following year, 1978, territories were mapped in Marley Wood. These are shown in Figures 3.2A and 3.2B. Figure 3.3 shows all box positions superimposed on the 100m national grid. In general the territories in Marley were not as well defined as those in Higgins' Copse. This may have been caused by the lower breeding densities (1.0 great tit pairs / ha, 1.7 blue tit pairs / ha) in Marley Wood, but could have been caused by differences in





Figures 3.2 A&B Great tit (A) and blue tit (B) territories in Marley Wood in late April 1978. The thin lines show the maximum observed extent of each territory. For great tits a mosaic is approximated with heavy lines.

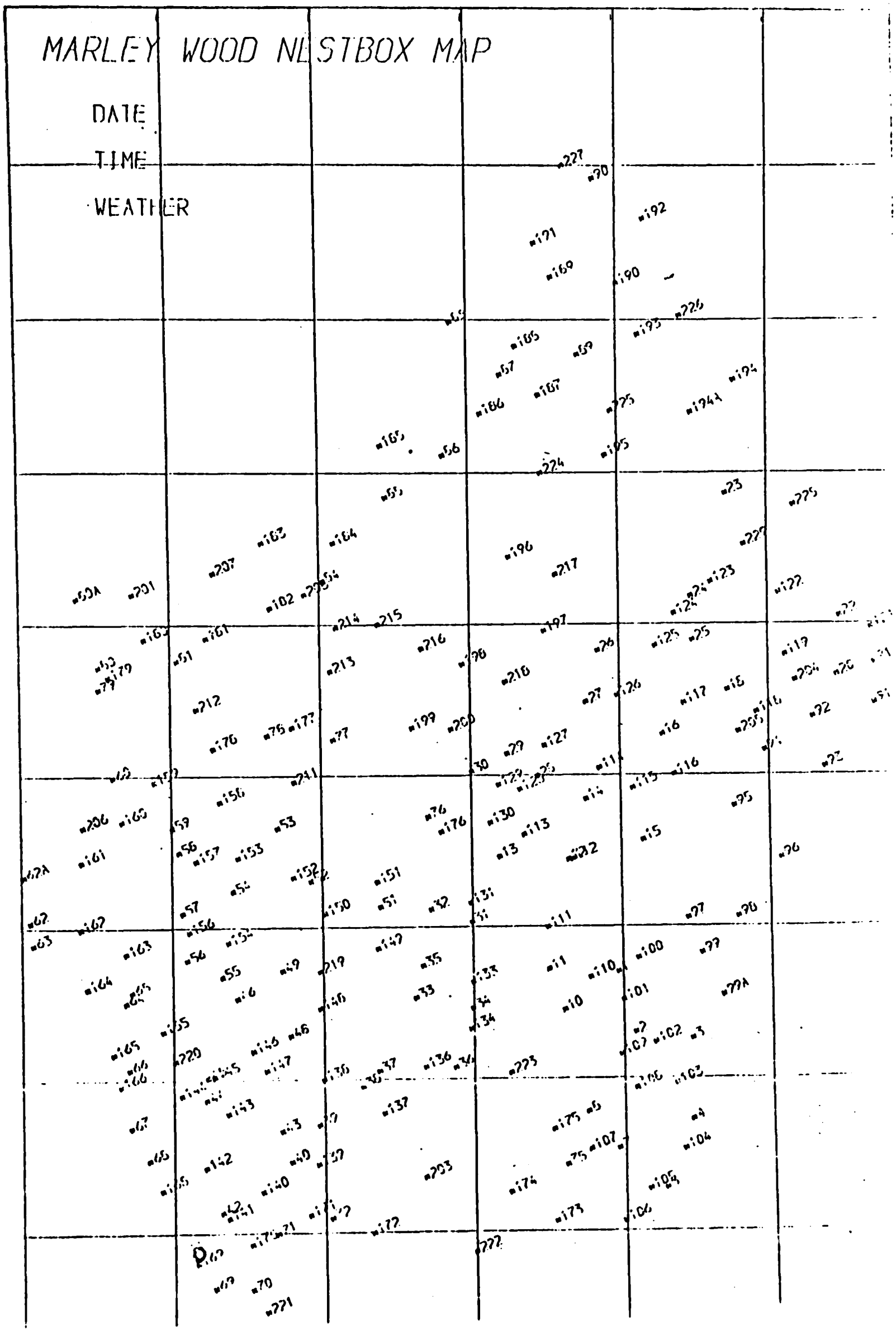


Figure 3.3. Grid map of Marley Wood showing the positions of all nest-boxes.

habitat or differences between the two years. The great heterogeneity of the habitats in Marley Wood may have tended to create more natural barriers between territories than in Higgins' Copse.

The thin lines in the figures of the Marley Wood territories show the maximum observed extent of each territory. For great tits a mosaic is approximated with heavy lines. For both species adjacent territories often did not touch. However, territories overlapped considerably in the areas of greatest density. Both blue and great tits nested at the greatest density in a strip south of the centre of Marley Wood, and this was the area where the greatest territorial activity was seen. Despite the lower densities in Marley Wood compared with Higgins' Copse, a similar picture emerges; blue and great tits tended to cover the wood with territories with no evidence of interspecific spatial separation or habitat segregation.

Nest-site spacing

Green (1979) used the 1977 data for nest-box occupation in Marley Wood together with the surveyed coordinates of nest boxes to determine the significance of intra- and interspecific spacing out of nest sites. He found that intraspecific interference in the selection of nest sites was significant, i.e., there were too few conspecifics nesting close to each other compared with a random occupancy of boxes. This is hardly surprising given that only one great tit (blue tit) pair could occupy a nest box within a great tit (blue tit) territory that included an average of about 7 (3) nest boxes.

Green found no significant evidence, however, for the overdispersion of interspecific nearest neighbour distances. Thus, blue and great tits apparently occupied nest boxes without interference from neighbours of the other species. This result is consistent with the overlap of great tit and blue tit territories. It also suggests that the intra-specific nest-site 'interference' probably arises indirectly from territoriality rather than through any knowledge of the positions of the nest sites of conspecifics.

Competition for nest boxes

Although there is no apparent interference in the interspecific spacing of nest sites, this does not mean that there is no competition for nest sites. A nest box is a very discrete, defendable and limited resource. It would be reasonable to expect that overt interspecific interference competition for boxes might be easily observed. In fact, in three springs in the woods I only saw two interspecific fights close to, and presumably for, nest boxes. Both fights lasted about 30 seconds, by far the longest interspecific fights I observed. However, even if every disputed box had several such interspecific fights associated with it, there would be little chance of observing more than a very few fights each year. Despite the value of a nest box as a resource, there is probably a high cost associated with continued fighting, especially to blue tits which are only about 60 percent of the size of great tits.

Rather than look for competition directly it is necessary to look for evidence of competition. One way to do this is to look for instances where one species has evicted

the other species from a nest site. This may be detected where one species has begun nesting and is then replaced by a second species. In the absence of any other information it is reasonable to assume that the probability of a great tit encountering a nesting blue tit equals the probability of a blue tit encountering a nesting great tit. If so the number of interspecific take overs should be equal for both species and independent of the breeding densities of the two species.

Taking the years 1971 to 1978 there were 16 instances where a great tit replaced a blue tit and 4 instances where a blue tit replaced a great tit. It appears that great tits are more likely to take over a blue tit nest than vice versa ($X_c^2 = 6.04$, $P < 0.02$). However, there is an element of asymmetry. Blue tits begin nesting before great tits by an average of 2.5 days and therefore it was less likely that a blue tit would encounter a great tit in a nest that it wanted than vice versa.

It is possible to make a crude estimate of the effect of the difference between the first egg dates of the two species. If, on a given day (d), $n_{d,a}$ pairs of species A begin nesting (or lay their first egg) and $\sum_{i=1}^{d} n_{i,b}$ members of species B have started nesting since the first day, then there are $n_{d,a} \sum_{i=1}^{d} n_{i,b}$ ways in which species A might take over a nest of species B. In an entire season (days 1 .... d) the number of possible ways for A to take over from B would be

$$\sum_{j=1}^{d} n_{j,a} \left(\sum_{i=1}^{j} n_{i,b} \right), \qquad (1)$$

and similarly B takes over from A would be

$$\sum_{j=1}^{d} n_{j,b} \left(\sum_{i=1}^{j} n_{i,a} \right). \qquad (2)$$

The ratio of the two estimates can be used to calculate the expected number of take overs by each species. It would be possible to lag $n_{i,a}$ and $n_{i,b}$ in (1) and (2) to allow species B and A time to establish the identity of the species originally occupying the nest box. This requires a lag of about 4 to 6 days. With or without such a lag the distributions of first egg dates for blue and great tits in 1971 to 1978 predict that approximately three take overs by great tits would be expected for every two by blue tits. Thus, for the 20 take overs observed, the expected is 12 by great tits and 8 by blue tits. The observed, 16 by great tits and 4 by blue tits, shows that there were still more take overs by great tits than expected, but that the difference was not significant ($X_c^2 = 2.55$, 1 d.f.).

A remaining factor, the niche width of box choice, might make the difference significant if a wider range of boxes was suitable to blue tits. However, the analysis of these data has already been stretched rather far for only 20 observations. It is best to look for other evidence of great tit dominance, preferably where data from before the nest construction period may be included. It is also necessary to determine the niche width of box choice for the two species by examining the use of nest boxes over a number of years.

Are nest sites used at random?

Before trying to develop any ideas about nest site selection it should be shown that the occupancy of boxes is

not just random between years. If the frequency distribution of observed use does not differ significantly from a random distribution, then any statement about nest site selection would be suspect. The 214 boxes in Marley Wood were chosen to study this question. These boxes have been in the same, or approximately the same, positions from 1960 to 1978. Boxes may be classified by the number of uses by blue and great tits. Table 3.2 shows the observed number of boxes that fell into each possible category of use. Given that each box could be used only once in each year by only one species, and given the total number of boxes available plus the number of boxes used by each species in each year, it is possible to calculate the predicted distribution of use under the null hypothesis of random occupancy of boxes (see methods). This was done using the data in Table 3.3 and the expected distribution is included in Table 3.2 for comparison with the observed frequency distribution of box use.

These distributions and the differences between them are best seen in Figures 3.4 and 3.5. The observed distributions deviate significantly from those expected under the null hypothesis. It is simplest to test the one-dimensional distributions shown in Figure 3.4. The chi-squared test was used to test the difference between the observed and expected distributions (blue tit, $X^2_9 = 180.7$; great tit, $X^2_9 = 327.8$; blue and great tits, $X^2_{10} = 705.7$; all $P < 0.001$).

The one-dimensional distributions show that certain boxes were used much more often than was expected. By necessity, there were also more than the expected number of

Table 3.2. Observed and predicted distributions of nest box use in Marley Wood for 1960-1978. For each cell observed is above predicted. Expected use less than 0.001 is indicated by a hyphen.

BLUE TIT \ GREAT TIT	0	1	2	3	4	5	6	7	8	9	10	11	12	13-19
0	0 .005	1 .042	3 .148	1 .324	1 .490	0 .543	2 .461	1 .307	1 .162	1 .069	0 .024	0 .007	2 .001	0 -
1	4 .039	7 .284	5 .945	5 1.924	3 2.693	2 2.774	3 2.171	2 1.324	1 .638	2 .245	0 .075	0 .018	0 .004	0 -
2	2 .134	3 .092	3 2.790	3 5.265	5 6.831	3 6.473	2 4.645	1 2.581	3 1.125	2 .387	1 .105	0 .022	0 .004	0 -
3	3 .283	3 1.765	4 5.053	1 8.825	5 10.546	6 9.158	3 5.986	2 3.006	2 1.172	2 .357	0 .084	1 .015	1 .002	0 -
4	2 .413	4 2.388	3 6.312	5 10.146	4 11.107	3 8.782	2 5.186	5 2.330	2 .804	0 .213	1 .043	1 .006	0 .001	0 -
5	0 .445	7 2.372	0 5.768	3 8.489	5 8.457	1 6.040	0 3.191	1 1.267	0 .380	1 .086	1 .014	0 .002	0 -	0 -
6	2 .366	4 1.796	3 3.996	1 5.349	3 4.812	3 3.074	5 1.435	0 .496	3 .127	0 .024	1 .003	0 -	0 -	0 -
7	1 .236	1 1.059	1 2.144	2 2.591	0 2.084	3 1.176	0 .478	1 .141	0 .030	0 .004	0 -	0 -	0 -	
8	1 .121	2 .494	0 .902	2 .975	2 .693	1 .340	1 .118	0 .029	0 .005	0 .001	0 -	0 -		
9	3 .050	0 .184	0 .300	3 .286	0 .177	0 .074	0 .021	0 .004	0 .001	0 -	0 -			
10	0 .017	0 .005	0 .079	1 .065	0 .034	1 .012	0 .003	0 -	0 -	0 -				
11	0 .004	0 .013	0 .016	0 .011	1 .005	0 .001	0 -	0 -	0 -					
12	0 .001	0 .002	0 .003	0 .002	0 .001	1 -	0 -	0 -						
13	0 -	0 -	0 -	0 -	0 -	0 -	0 -							
14	0 -	1 -	0 -	0 -	0 -	0 -								
15	0 -	1 -	0 -	0 -	0 -									
16-19	0 -	0 -	0 -	0 -										

Table 3.3. Number of blue and great tit pairs using the 214 nest boxes in Marley Wood from 1960 - 1978.

YEAR	BLUE TIT	GREAT TIT	TOTAL
1960	26	65	91
61	64	94	158
62	20	45	65
63	39	41	80
64	40	66	106
65	48	45	93
66	51	52	103
67	34	34	68
68	34	41	75
69	33	45	78
1970	30	43	73
71	35	57	92
72	31	44	75
73	50	46	96
74	68	35	103
75	65	36	101
76	39	13	52
77	81	30	111
1978	41	28	69
TOTAL	829	860	1689

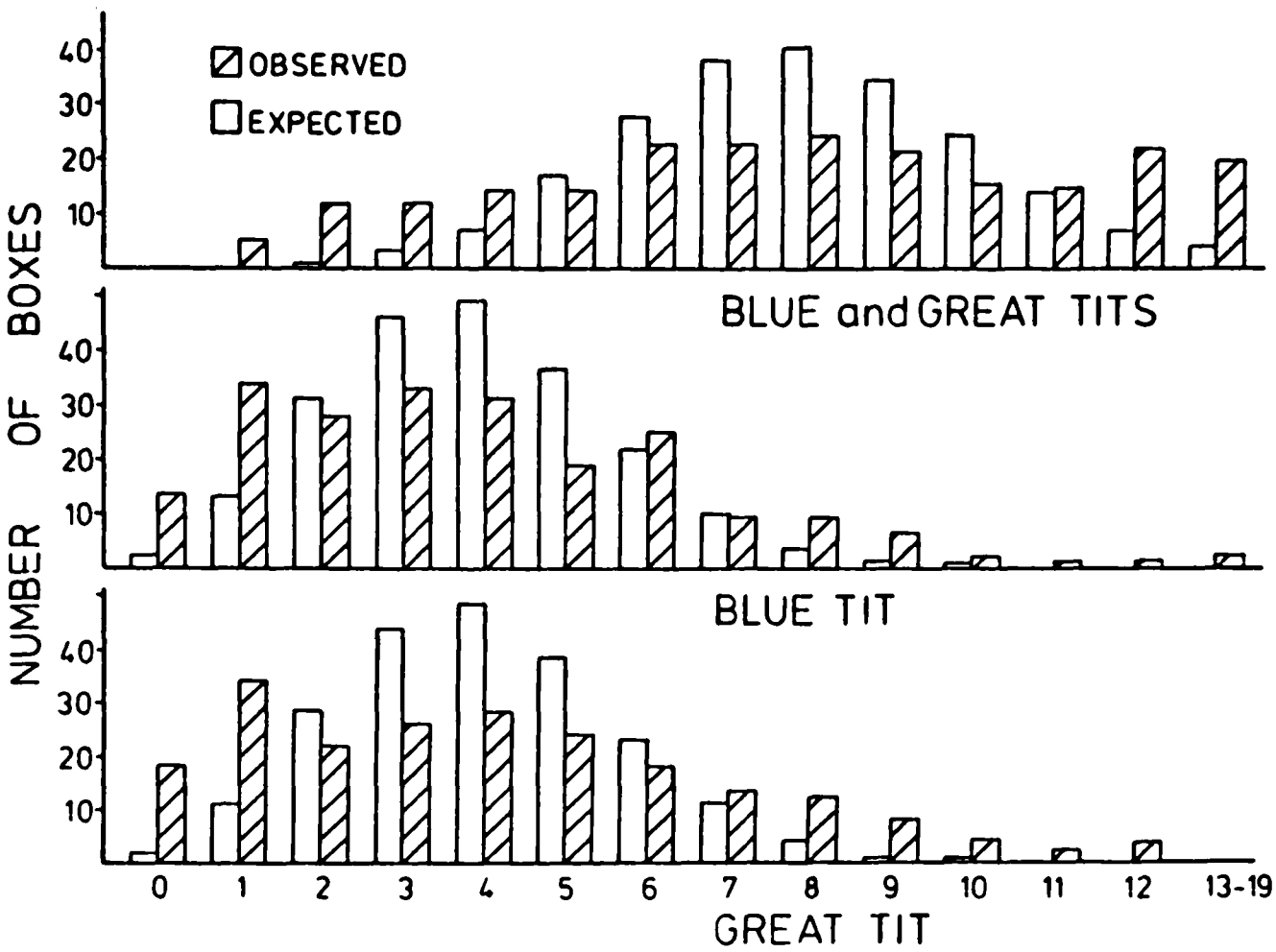


Figure 3.4 Observed and expected distribution of use of nest boxes by blue and great tits (1960 - 1978).

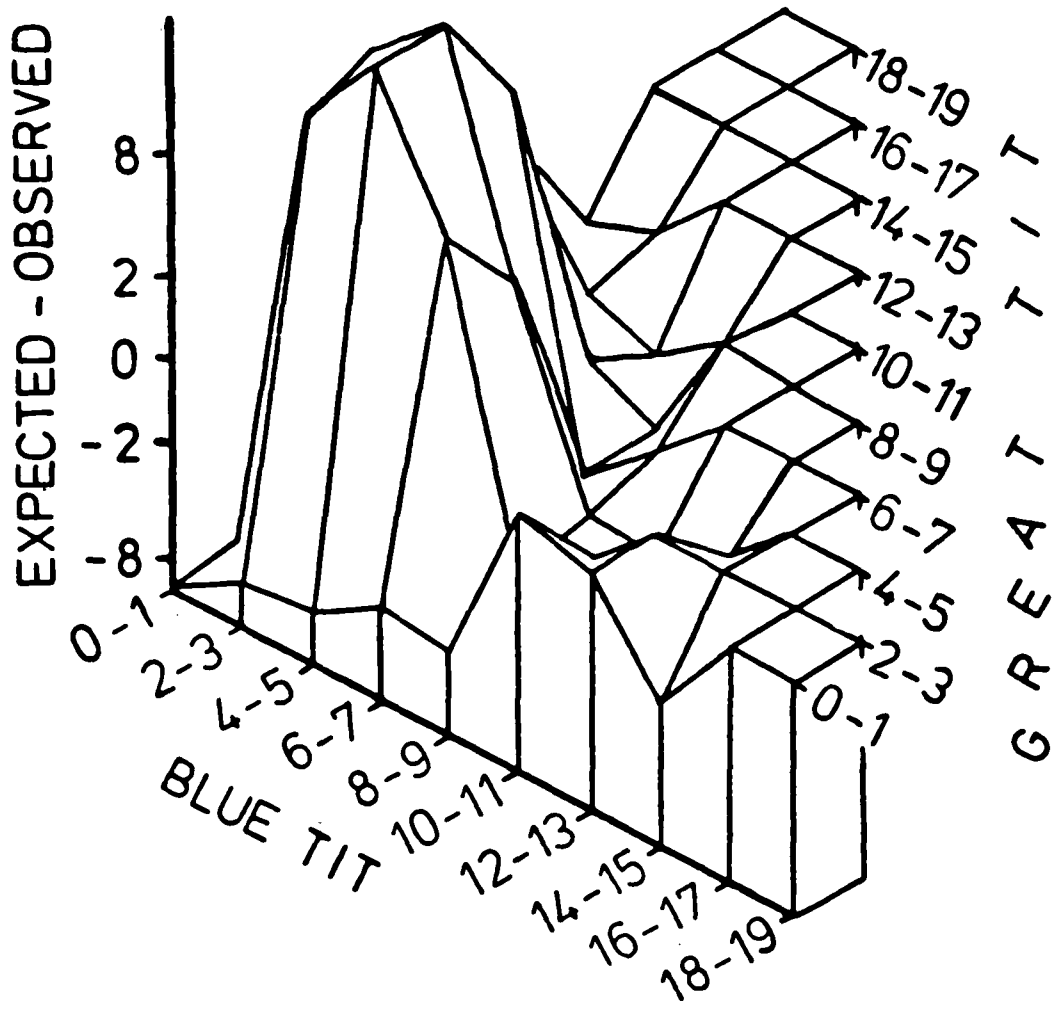


Figure 3.5 Deviation of box occupancy from the expected random distribution. The blue tit and great tit axes categorize boxes by the number of times they were used by each species. The vertical axis shows the deviation from expected for each blue tit - great tit combination.

seldom used boxes. In addition, the two-dimensional distributions show that there were more than the expected number of boxes used by one or the other species and there were also more than the expected number of boxes used frequently by both species. The last two points are especially important for they imply that while there may be some habitat segregation between the two species, there is probably competition for many of the boxes.

Aside from random effects, there are probably three main reasons why some boxes are used more than others. 1) The habitat at or around certain boxes may be particularly suitable to one or both species. 2) Boxes are used by the same pair for several years, especially if the pair has been successful in rearing young. 3) The boxes are chosen according to the area around each box for which that box is closer than any other (the Dirichelet tessellation or Voronoi polygon for each box), i.e., boxes at a low density are more likely to be used. All three reasons appear to be significant (Minot, P.Green and Perrins, in prep.), but the one important feature for this discussion is that selection of boxes leads to the potential for competition.

Nest site choice and niche width

The observed distributions of box use by great tits and blue tits are very similar (Figure 3.4). If these are plotted on the same graph, the blue tits tend to be slightly higher in the range of 2 - 6 uses while the great tit is higher at 0 uses and 7 - 19 uses (Figure 3.6). However, the expected random distributions for the two species are

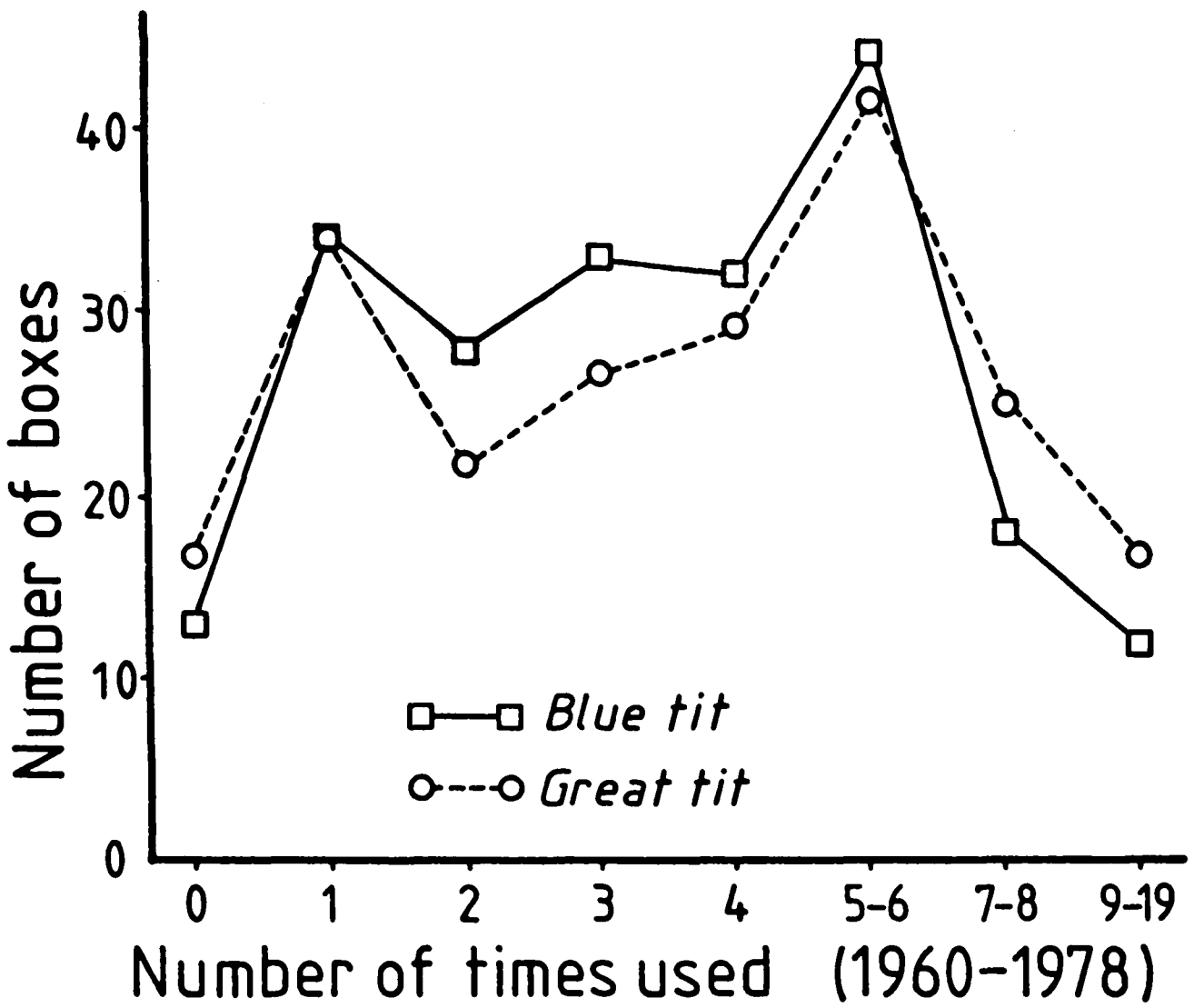


Figure 3.6 Comparison of the distribution of uses of boxes by blue and great tits.

different so direct comparison of the distributions is not meaningful. It is possible to compare the deviations of the two observed distributions from their expected random distributions. This is done in Figure 3.7. Again, it appears that, overall, great tits tend to be more selective in their choice of nest sites than are blue tits. This result is consistent with great tits getting the boxes they 'want'. It may also be that blue tits occupy a broader niche and find a wider range of boxes to be suitable. Finally, the larger territories of great tits will give individual great tit pairs a wider range of boxes from which to choose.

Competition for favoured boxes

If interspecific competition does occur it is more likely to occur in years of high population density of both species because this is when contact between the two species would be greatest and the availability of alternate sites the lowest. The greatest competition should occur for those boxes which have been most popular with the two species. Taking the 19 years in Marley Wood from 1960 to 1978, a popular box may arbitrarily be defined as one used at least 10 times and at least twice by each species. There is a total of 62 such boxes. In 1961, a year of exceptionally high blue and great tit densities, 40 great tit and 13 blue tit pairs occupied 'popular' boxes. For the years 1960, 1962 - 1978 this category of boxes was used by 292 of the 765 blue tits and 298 of the 766 great tits, i.e., 1.021 great tits / blue tit in the popular boxes and 1.001 great tits / blue tit in the whole wood. If the 64 blue and

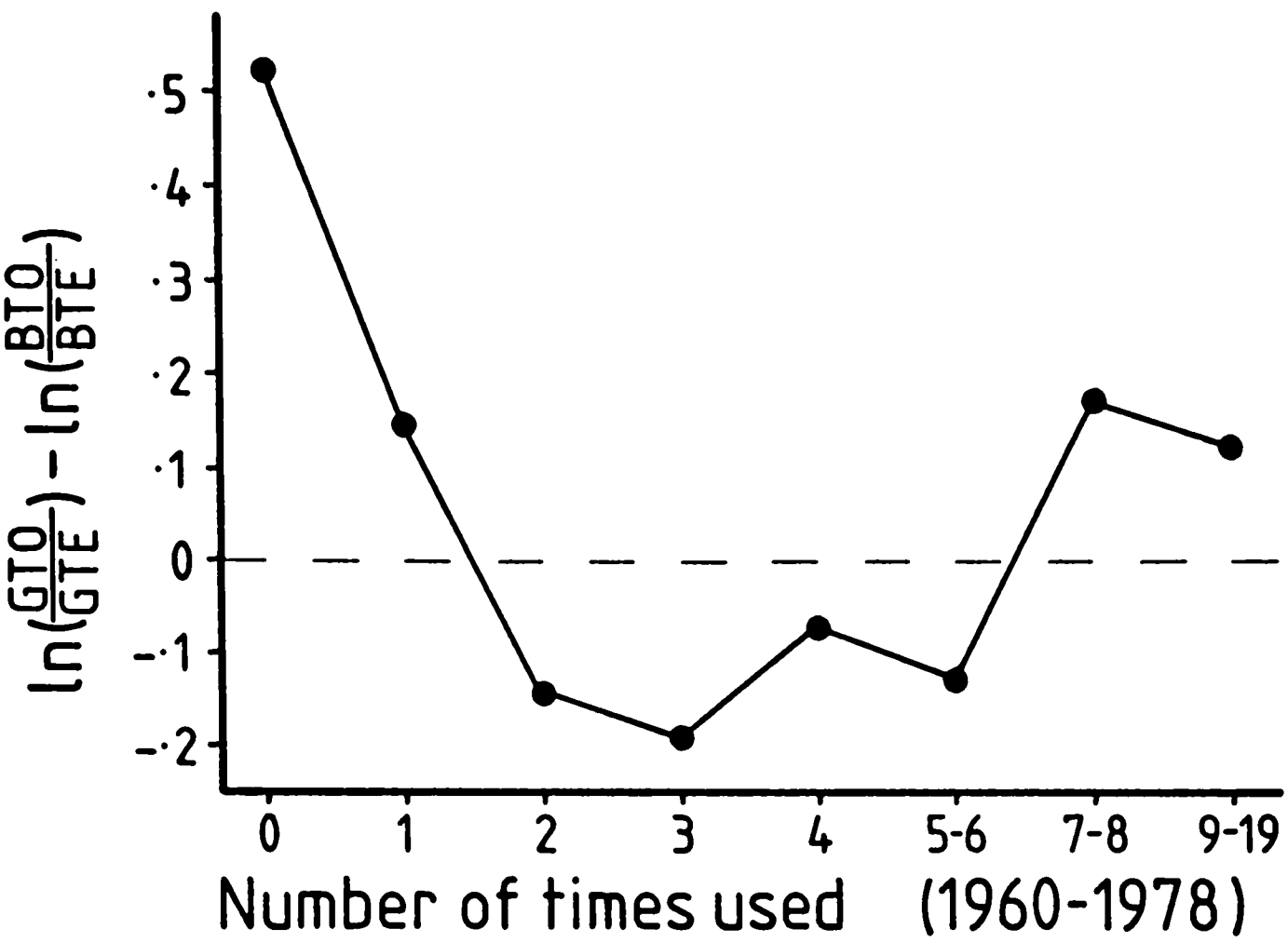


Figure 3.7 Difference between the blue tit and great tit distributions of use of boxes corrected for expected random distributions. GTO and GTE (BTO and BTE) are the observed and expected number of great tits (blue tits).

94 great tits in 1961 took the popular boxes in proportion to the average use of popular boxes by the two species, and in proportion to the numbers of each species in the wood, the expected ratio of use would be (1.021 / 1.001) x (94 / 64) = 1.498 great tits / blue tit in 1961. With 53 of the popular boxes used in 1961 there should have been 21.2 blue tits and 31.8 great tits in the popular boxes. The observed ratio of 40 great tits to 13 blue tits is significantly higher than expected (X^2_c = 4.67, $P < 0.05$). This result confirms the a priori expectation that great tits were dominant in obtaining nest sites in this one high density year.

A similar analysis was tried for 1977 when there were 81 blue tits and 30 great tits. There was no significant departure from the expected ratio of blue tits to great tits using the 'popular' boxes.

Density dependence of competition

From the above discussion it is clear that it is primarily the great tits that dominate interspecific competition for nest sites. It is reasonable to expect the effect of great tits on blue tits to vary with great tit density rather than to occur only in 1961, the highest density year. The most likely boxes to be affected by great tit density are those most popular with blue tits but also used by great tits.

In Marley Wood there were 39 boxes used at least six times by blue tits and at least twice by great tits from 1960 to 1978. Each box may be assigned a score of relative popularity, the proportion of use by blue tits of all

uses by the two species over the 19 years. Thus, a box used seven times by blue tits and three times by great tits would have a score of 0.70. For each year 1960 to 1978 the mean score for all blue tit occupied boxes was computed. If great tits are affecting the choice of boxes by blue tits the annual mean score for relative popularity should increase as the number of great tits increases. That is, as the number of great tits increases the blue tits should be forced to use those boxes relatively less popular with great tits. This is what happens (Figure 3.8). The breeding density of blue tits may also affect the blue tits' choice of boxes. The partial correlation of box score with blue tit density is not significant, but it is negative as would be expected if more blue tits meant that the extra blue tits had to use the less favoured boxes (Table 3.4).

CONCLUSIONS

The results of territory mapping in Higgins' Copse and Marley Wood showed that blue and great tits established territories that overlapped. There was no evidence of interspecific territoriality or habitat segregation. Perhaps the only distinguishing feature of the territories of the two species was that great tit territories were larger than blue tit territories.

It is difficult to make much of the three blue tit pairs in Higgins' Copse that nested in natural sites. Two occupied territories with no nest boxes yet the third moved from a nest box to a natural site leaving a second box within its territory vacant. Those three pairs probably

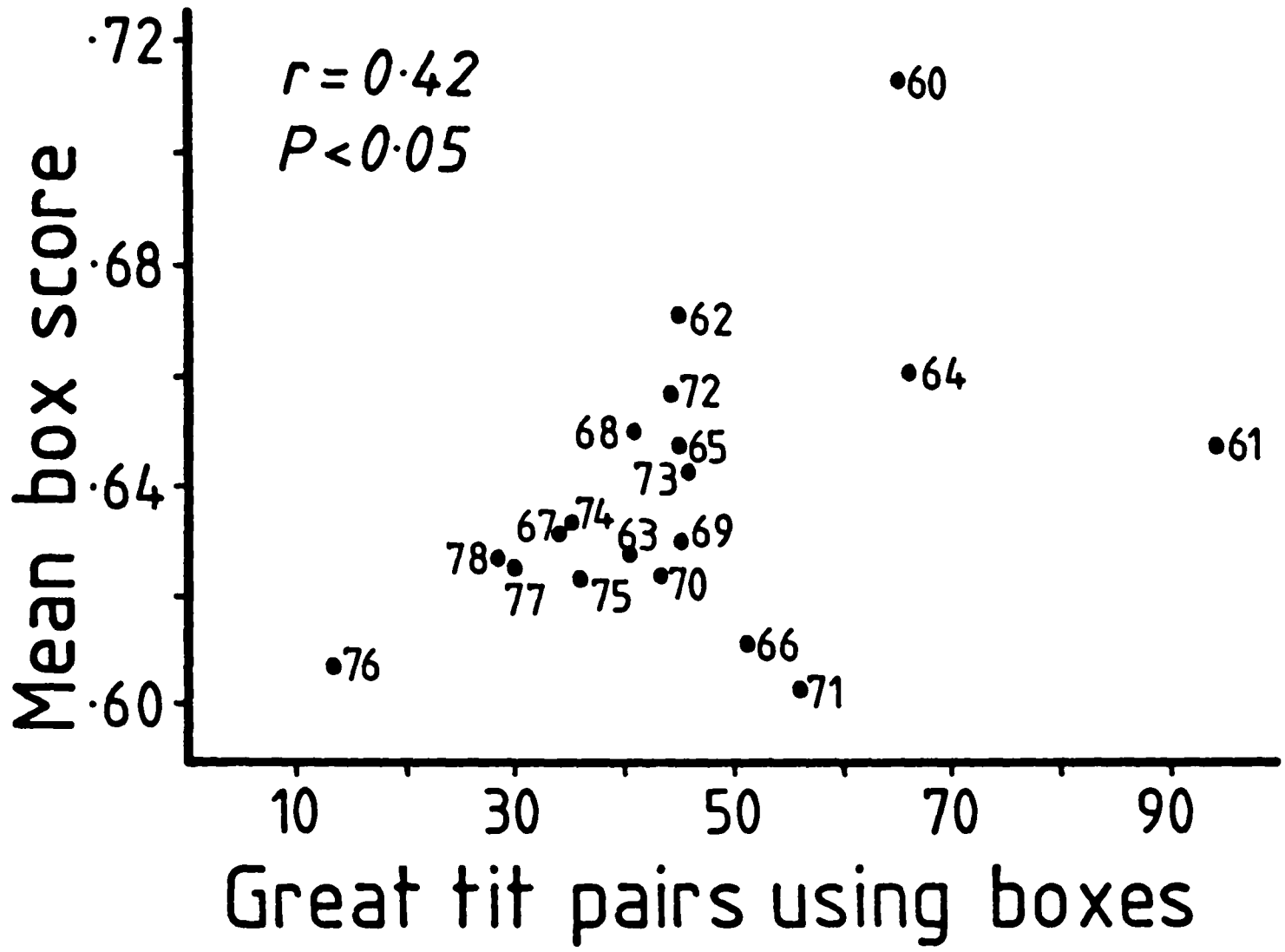


Figure 3.8 Effect of great tit numbers on the mean box score for blue tits. See text for an explanation of mean box score.

Table 3.4. Effect of number of blue and great tits on the annual mean blue tit box score. See the text for an explanation of the box score. The regression is based on 19 years data.

	Coefficient	t-test	P<
Constant	0.633	30.01	0.001
Number great tits	0.000636	2.04	0.05
Number blue tits	-0.000530	1.59	0.10

21 percent of variance accounted for

reflect a general difference between blue and great tits. The smaller territories of blue tits probably result in more blue tits left without a nest box in some areas, especially in a year with high nesting densities. However, blue tits may not favour nest boxes over natural sites to the same extent as great tits. Certainly in Marley Wood, with the high density of nest boxes and comparatively low breeding density of 1978, no blue tits were known to be nesting in natural sites. Whatever the causes for blue tits occasionally using natural sites, most blue tits and almost all great tits have used nest boxes, particularly in areas like Marley Wood where the boxes have been provided at an average density of eight per hectare.

The abundance of artificial sites has meant that boxes *per se* have not been a limiting resource. However, several lines of evidence have suggested that there is competition for the boxes and that the larger great tits apparently dominate the contests with blue tits. The difficulty in demonstrating the competition underscores the general abundance of nest boxes. Nevertheless, certain nest sites were popular with both species and competition for these appeared to increase as the number of blue and great tits increased. Experimental verification of the effect of breeding density would be difficult because increasing the breeding numbers would be almost impossible. Changing the number of available boxes would achieve a similar end. However, the interpretation of the results of such an experiment would have to account for the differences in blue tit and great tit territory sizes. A more revealing

experiment might be to remove all boxes except those known to be very popular or very unpopular with both blue and great tits to see if there was a change in the predicted ratio of use by the two species.

Interspecific interference competition could not be detected in the spacing of the nesting sites of blue and great tits. This result and the fact that blue and great tit territories overlap, indicate that any interspecific isolation of breeding resources may be very limited prior to nesting. With little or no apparent interspecific spatial separation there may be direct competition for resources. This appeared to be the case for specific nest sites. In the next chapter it is shown that there is also scramble competition for food during the breeding season.

CHAPTER 4

Competition for Food

In order to demonstrate the potential for competition between two species (or individuals) for food, it is necessary to show that the presence of one species inhibits the foraging success of the other. Three criteria ought to be met if scramble competition for food occurs. First, the ability to feed should be limited by the abundance of food. Second, feeding should cause a decrease in the availability of food. And third, the foods eaten by one species otherwise could have been eaten by the second species.

Winter is often thought to be a period when competition for limited resources is most severe. In contrast, the breeding season often coincides with an abundance of food. At times the density of potential prey items suggests that food is superabundant. For example, Varley et al. (1973:121) report that densities of winter moth (Operophtera brumata) larvae in some years exceed 200 m^{-2} in the canopies of oaks (Quercus robur) in Wytham Wood. It is tempting to equate this abundance with a relaxation of competition. However, this abundance often has a short duration and it may vary considerably between years. Also, adults need to rear as many young as possible with a minimum of stress to themselves in order to be reproductively successful. This requires that they be able to feed as efficiently as possible. Consequently, depletion of the food resource could lead to competition between individuals. Similar prey items may be taken by many breeding species and

this could result in diffuse competition (MacArthur 1972) amongst the bird species that use similar foods.

To what extent is competition for food, either within or between species, likely to be important during the breeding season? All of the necessary criteria for competition outlined in the opening paragraph of the chapter have been demonstrated for great tits or blue tits during the breeding season. Royama (1970) showed that insect abundance limited the breeding success of great tits. Betts (1955), Gibb and Betts (1963), and Tinbergen (1949) estimated that depletion of food by tits alone ranged between 1 and 37 percent. Tinbergen (1960) presented data which suggest an almost total overlap in the diets of nestling blue and great tits in pine woods.

This chapter looks primarily at the feeding overlap between blue and great tits and examines the extent to which competition between the two species might be expected based on similarities of their feeding behaviour. I review evidence which shows that the feeding sites of the two species changed with season and that they were most similar during the nestling and post-nestling periods (May - August). Direct interspecific aggression was most common during the period November to March, the time when feeding site overlap was lowest. Finally, an examination of foods brought to the nestlings shows that there was a high overlap in the prey items of the two species.

METHODS

Nest-box cameras

Great tits and blue tits feed their young on fairly large prey items such as caterpillars of moths, spiders and daddy longlegs (Tipulidae) which are carried to the nest in the bill. This means that prey items are visible as a bird enters its nest. Tinbergen (1960) used this feature to record prey items by sitting in a hide attached to a nest box and watching the bird as it entered. Royama (1959, 1970) designed a camera system to automatically record each visit to the nest by photographing the bird as it entered. The advantage of this technique is that continuous observations may be made at several nests and that each photograph may be studied for as long as necessary to identify the prey item(s). Royama's system was based on a 16-mm cine camera with electronic flash. It was expensive and awkward to use but produced records of high quality.

The system I used was based on a super 8-mm cine camera (Minolta model XL-400 and XL-401). The cameras come equipped with electronic remote shutter release and electronic flash synchronization. The camera was put into the back of a specially constructed nest box. A micro-switch at the entrance was closed each time a bird entered or left the box. The switch triggered the camera and synchronized flash (Figure 4.1). A watch was put next to the entrance hole so that the time and date of each photograph (visit) was known. The camera was run on batteries and a mains supply was used for the flash. A storage battery would have been needed in the absence of a mains supply because

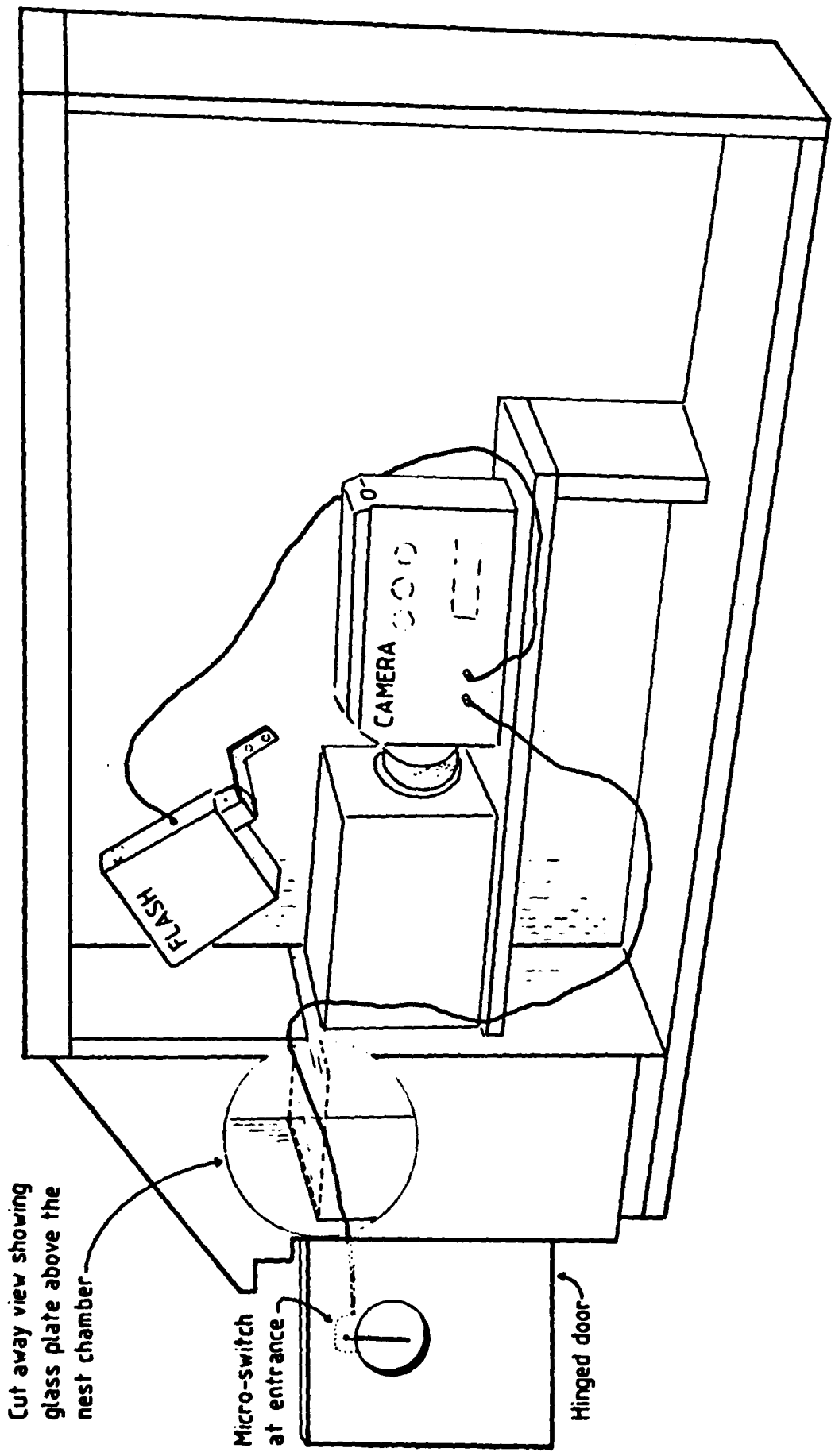


Figure 4.1 Nest box with camera.

the flash used four AA-size alkaline cells for every ca. 100 flashes.

In the early morning the camera lens tended to fog. This was particularly a problem on cold mornings and was exacerbated by older, larger broods which produced more moisture. Silica gel helped but the only real solution was to put a 15-watt light bulb, covered with foil, in the back of the box. This was left on day and night. A smaller bulb, perhaps 0.5 watt, directly under the camera lens would probably work just as well and might be run off a storage battery.

One 15-m cassette of film lasted 2-5 days depending on the feeding rate of the parents and produced ca. 3500 frames, half of which were birds entering the nest.

The camera system was not without some minor problems. 1) The parents did not always trip the switch at the same distance from the camera thus some photographs were out of focus. 2) The resolution on a frame of super 8-mm film is low and the optics of the camera were not excellent. 3) The recycling time for the flash was from 5 to 20 seconds so blank frames resulted from tripping the micro-switch during the recycling time. 4) The flash units, designed for 35-mm cameras, could not stand up to very heavy use and after ca. 10-15,000 flashes pictures got very noticably darker. This could be corrected in part by replacing the discharge tube.

Overlap indices

Various methods have been devised to measure the overlap between different features of two species. These are variously called competition coefficients or indices of overlap and may be used to indicate the extent of similarity between two species, e.g. food selection or habitat preference. Two commonly used indices are:

$$\alpha = 2 \sum_i a_i b_i / (\sum_i a_i^2 + \sum_i b_i^2) \qquad (1)$$

and

$$\alpha = \sum_i a_i b_i / (\sum_i a_i^2 \sum_i b_i^2)^{\frac{1}{2}} \qquad (2)$$

where a_i (or b_i) is the use of the ith resource by species A (B) as a proportion of all resources used by species A (B). Both indices are discussed by May (1975) and (1) by Horn (1966). While both have advantages, I shall use (1) which tends to give lower values than (2). The index varies from 1.0, total overlap, to zero, no overlap.

The index may be used in either a single resource dimension, e.g. prey species; or in several dimensions, e.g., tree species and foraging height. In the multidimensional case it is best used with a full factorial number of elements, e.g., in the two dimensional example with n tree species and m foraging heights there should be nm categories used to calculate α.

One dimensional α's may be combined by multiplying them but the true multidimensional α may be higher if the one dimensional α's are not independent or in certain cases even lower than the products of the single

dimensions (May 1975).

Gibb (1953) used an asymmetric measure of overlap which he called 'percentage segregation'

$$\%S = 100 - \frac{(\Sigma a_i)^2}{A \Sigma a_i^2 b_i^{-1}} \times \frac{N_A}{N_B} \times 100, \qquad (3)$$

where a_i = number of species A feeding on the ith substrate,

b_i = number of species B feeding on the ith substrate,

A = total number of species A seen feeding, and

N_A, N_B = total numbers of species A and B in the woods.

As a first step in analysing this index, it may be simplified to more closely resemble the overlap index (1), discussed above.

$$\alpha_{a,b} = \frac{(\Sigma a_i)^2}{A \Sigma a_i^2 b_i^{-1}} \times \frac{N_A}{N_B} \qquad (4)$$

One obvious problem with (3) and (4) is that they require accurate information about the number of species A and B in the area. Even if this is known, it is possible to have an overlap value greater than one if species A is less visible than species B. For this reason it might be better to use the total number of species A and B seen, i.e., $A = \Sigma a_i$ and $B = \Sigma b_i$. Then the index would become

$$\alpha_{a,b} = \frac{A^2 B^{-1}}{\Sigma a_i^2 b_i^{-1}} \quad . \qquad (5)$$

A second problem associated with (3) - (5) is that the index weights extremely heavily those instances where the ratio of a_i to b_i is very high even if a_i and b_i are small compared with Σa_i and Σb_i. Note especially that instances where b_i=0 can not be included as $a_i^2 b_i^{-1}$ would

be undefined, though the corresponding a_i would be included in A. Again, in such instances it would be possible to have $\alpha_{a,b} > 1$ (or %S < 0).

The primary advantage of the index is that it takes some account of the niche width. Where species X uses a particular substrate frequently but species Y uses it very little, the overlap of X with Y ($\alpha_{x,y}$) will tend to be lower than Y with X ($\alpha_{y,x}$), all else being equal.

Gibb (1953) used full factorial, two dimensional (tree species x part of tree) feeding site use to compute his overlap indices. Unfortunately, he does not present the raw data for conversion to an overlap index in the form of (1) or (2). Consequently, I present his results in the form of (4), despite the problems associated with the interpretation of the index.

RESULTS AND DISCUSSION

Feeding site overlap

The potential for competition for food between two species can be measured by the overlap in feeding areas of the two species. If two species feed in the same places then it is more likely that they are hunting for the same food than if they forage in different places. Two studies in Wytham have compared the feeding sites of the various tit species at different times of Year (Gibb 1953, and Hartley 1953).

Hartley examined three aspects of the feeding place; height above ground, tree species and part of the tree (branch, twig, etc.). Hartley presented the results

separately for each of the three aspects. I have taken his data and calculated overlap coefficients. Hartley documented the change in feeding heights on a monthly basis. The change in overlap is shown in Figure 4.2. During the coldest months, December to March, the overlap in feeding heights was lowest. During this time about 40 percent of the great tits were feeding on the ground versus only 2 percent of the blue tits. This difference in time spent feeding on the ground was largely responsible for the low overlap from December to March, but of the birds feeding in trees the great tits were lower than the blue tits.

Hartley also documented differences in the use of different parts of the tree and different tree species, but only by each quarter of the year. The overlap coefficients for all three aspects are summarized in Table 4.1. The parts of the tree used by blue and great tits hardly differed in any of the four quarters. However, Morse (1978) found differences between the two species in December 1972 and January 1973 ($\alpha = 0.76$). At least from Hartley's data, tree species and feeding height were the most important of the three aspects separating the two species.

It is unlikely that these two aspects were independent. Great tits tended to forage more in elder and sycamore which were not as tall as the oaks preferred by blue tits. Such a lack of independence makes it difficult to compute an overall coefficient of overlap even with only two resource dimensions. The multidimensional overlap probably falls between the mean and the product of the individual

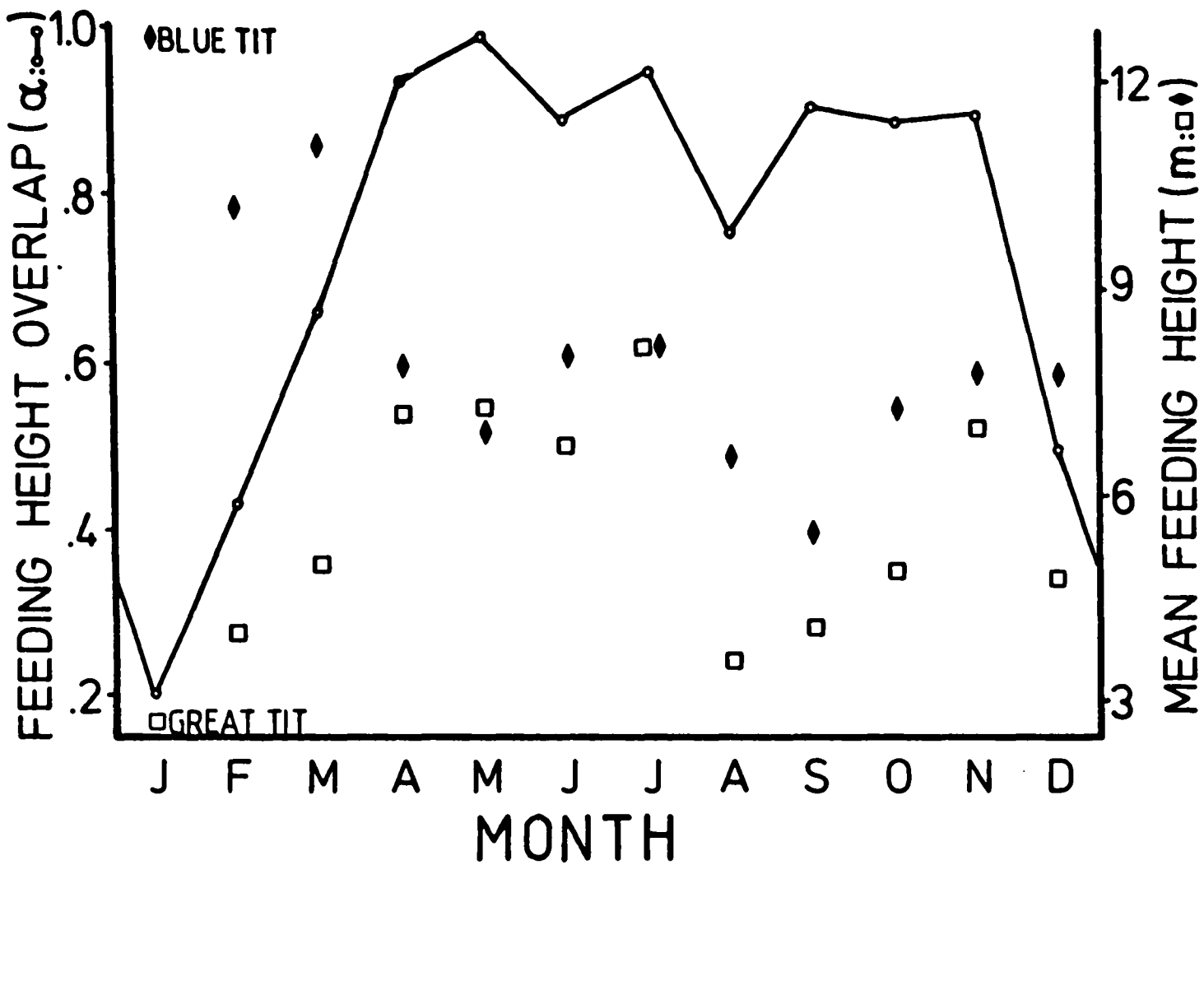


Figure 4.2 Effect of time of year on feeding height overlap and mean feeding height. Data from Hartley (1953).

Table 4.1. Seasonal changes in the overlap coefficients of feeding blue and great tits (data from Hartley 1953).

	JAN-MAR	APR-JUNE	JULY-SEPT	OCT-DEC
Tree species (α_1)	.80	.95	.75	.96
Height (α_2)	.40	.98	.91	.82
Tree part (α_3)	.99	.99	.99	.99
Mean (α_1, α_2)	.60	.97	.83	.89
Product ($\alpha_1 \cdot \alpha_2$)	.32	.93	.68	.79

coefficients. Table 4.1 includes the two-dimensional means and products for tree species and height.

Gibb (1953) also looked at the overlap in the feeding sites of blue and great tits. He collected data in two dimensions, tree species and part of the tree. However, his data consisted of a two-dimensional matrix rather than just the sums in each dimension separately. Thus categories consisted of oak leaves, oak branches, oak twigs, oak trunk, hazel leaves, hazel branches, ... etc. Such a full factorial matrix is much more valuable in detecting differences between species. Gibb's data, like Hartley's, came from Marley Wood and they show a generally similar pattern (Figure 4.3). The index Gibb used was quite different from the one I used on Hartley's data but the annual trends should be the same. Gibb found a much lower overlap from September to December than Hartley's data would suggest and this might reflect the complete matrix approach of Gibb or differences between the years of observation. It is more likely that the main difference is in the natures of the two different overlap indices used. The consistent parts of the two sets of data are that overlap is very low during the winter and quite high during the nestling and post-fledging period. There is probably a decrease in overlap beginning in July or August.

Interspecific aggression

If actual competition varies with season than there may be a change in the behaviour of the birds. As competition increases the level of aggression between

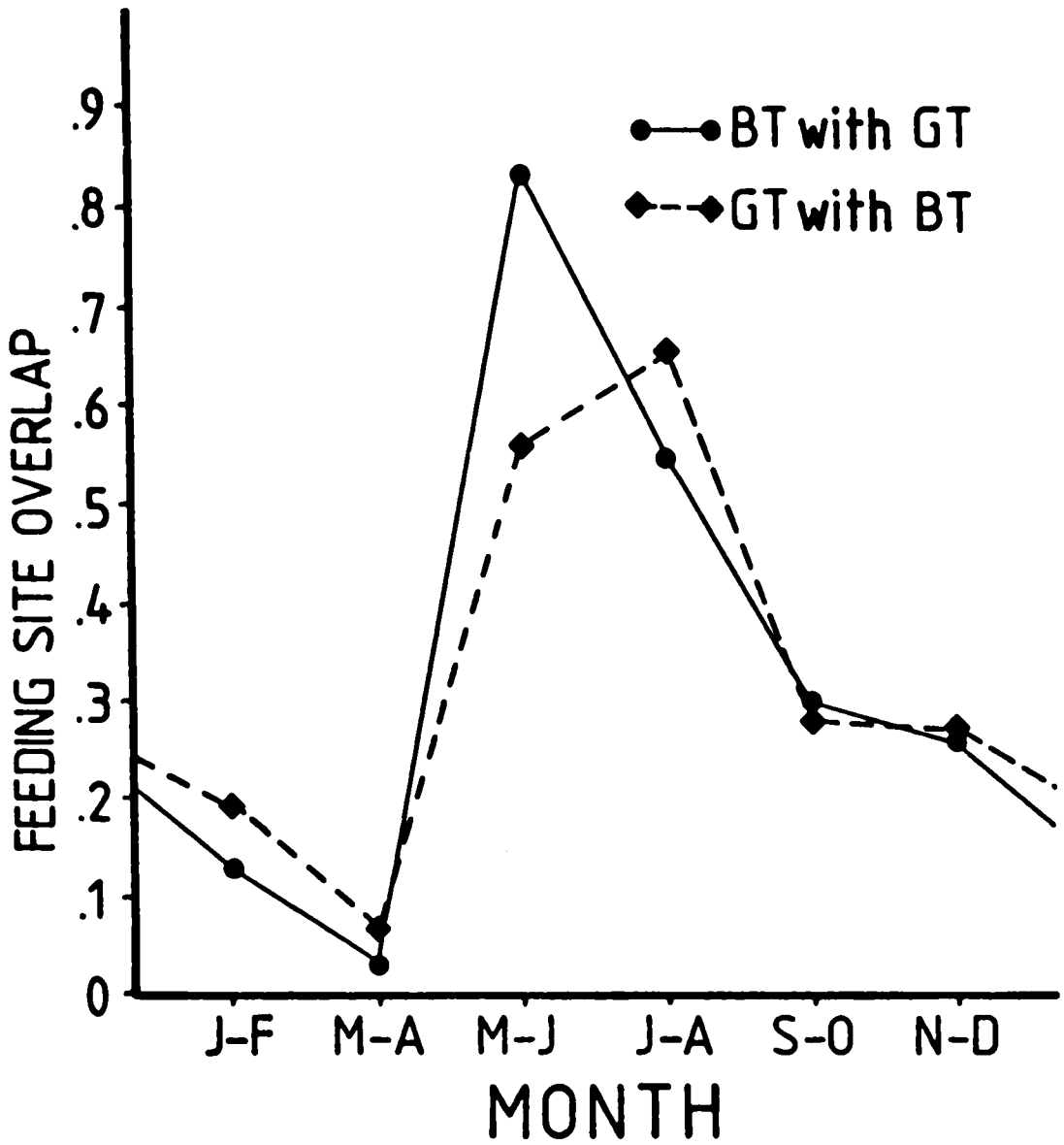


Figure 4.3 Effect of time of year on feeding site overlap. Feeding site overlap was calculated from the use of tree part and tree species. The overlap index used is the directional index derived from Gibb's (1953) measure of percentage segregation. Data from Gibb (1953).

individuals may increase as well. Hinde (1952) looked at the change in the rate of supplanting attacks by great tits with season and found that they were much less common in summer than in winter (Figure 4.4). They were mostly directed toward conspecifics in June to August, but from September to February they were directed at congeners, largely the blue tit. Gibb (1953:85) found that interspecific attacks by great tits were most common in March and April though Hinde reported that most occurred in 'mid-winter'.

One problem with the observation of attacks in the period March to May is that they may be for resources other than food. Interspecific attacks may be for nest sites. I have only observed two interspecific fights between blue tits and great tits which lasted for more than 10 seconds. Both were within a few meters of a nest box that was later occupied.

I observed supplanting attacks at feeders near mist nets in Higgins' Copse in March and April 1977. Because the food source was artificial it is difficult to compare my results with Hinde's data, but it is possible to look at inter- versus intraspecific supplanting attacks. The first observation period was for 11 hours during the period 9-12 March 1977. The results are shown in Table 4.2a. The supplanting species was not independent of the supplanted species. Intraspecific supplanting attacks occurred more than expected. Similar results were obtained in 14 hours observation during the period 11-13 April 1977 (Table 4.2b). However, the overall rate of supplanting attacks decreased

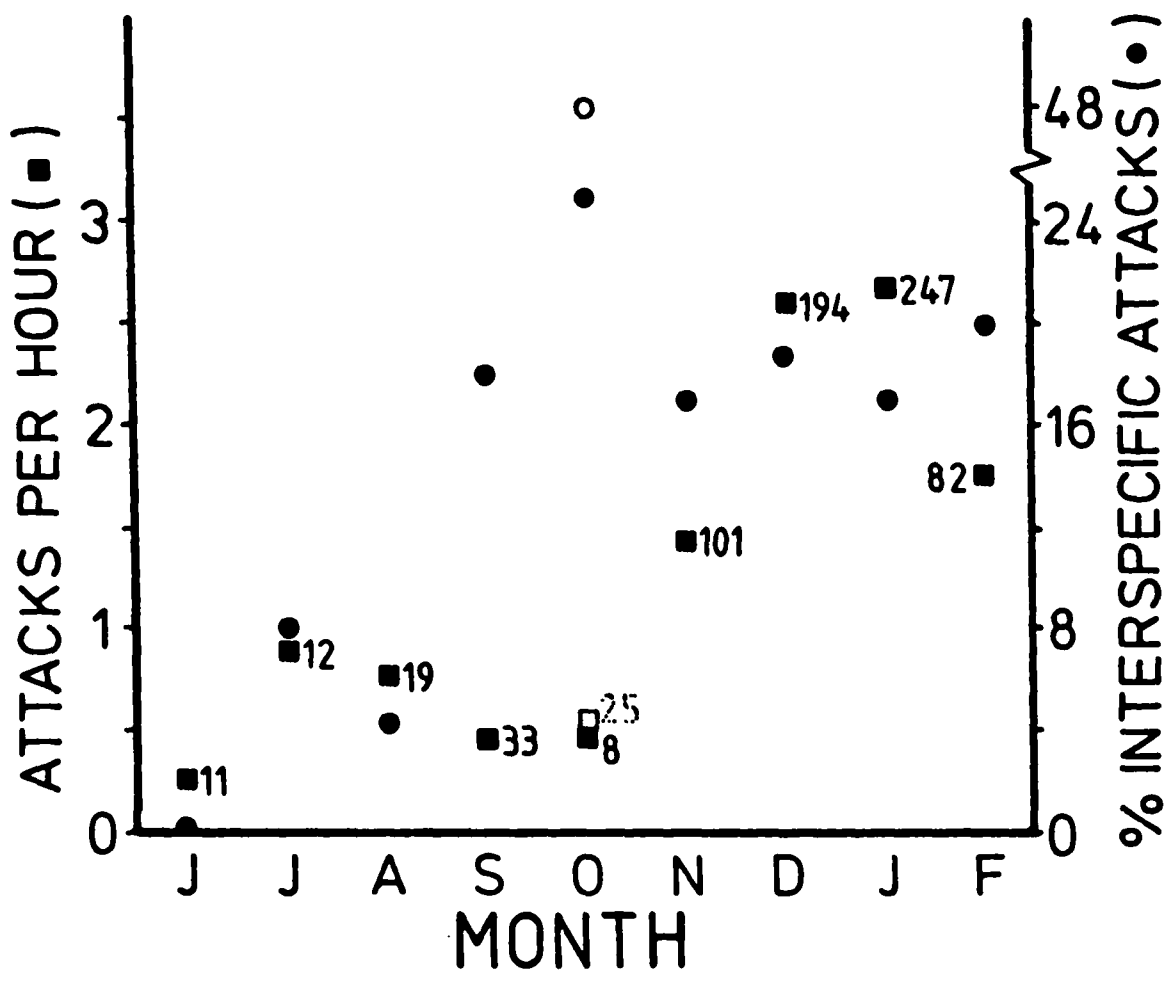


Figure 4.4 Effect of time of year on the attack rate and percentage interspecific attacks by great tits. The number of attacks observed is shown against the attack rate. The open symblos for October indicate some questionable data. Data from Hinde (1952).

Tables 4.2 a+b. A comparison of supplanting versus supplanted species at artificial feeding stations in Higgins' Copse. GT is great tit and BT is blue tit.

a. Eleven hours observation on 9-12 March 1977. Observed (Expected)

Supplanted Species	Supplanting Species: GT	Supplanting Species: BT	Total
GT	20(15.5)	1(4.5)	20
BT	28(32.5)	14(9.5)	42
Total	48	14	62

$X_c^2 = 5.36$

$P < 0.025$

B. Fourteen hours observation on 11-13 April 1977. Observed (Expected)

Supplanted Species	Supplanting Species: GT	Supplanting Species: BT	Total
GT	17(12.1)	0(4.9)	17
BT	13(17.9)	12(7.1)	25
Total	30	12	42

$X_c^2 = 9.19$

$P < 0.01$

from 5.6 to 3.0 attacks per hour. Presumably, natural food sources were becoming more abundant by April.

Comparing the two types of interspecific supplanting attack, the instances of great tits supplanting blue tits far exceeded the reverse. This may be because it was worth competing for the large, artificial food supply and the great tits, being larger, were better at supplanting than the smaller blue tits. In the natural situation this asymmetry apparently disappears (Table 4.3). In comparing artificial feeders to natural conditions Garnett (1976) noted that 'in the natural situation the food is much more dispersed than in the experimental set up. As a result, aggressive interactions are less common in natural conditions'. In addition to being more dispersed, the smaller naturally occurring food items may not be worth fighting over and interspecific supplanting attacks may occur largely by mistake except possibly in mixed species flocks which form during the winter.

In summary, overall attack rate and the percentage of interspecific attacks is probably lowest from about May to August. This is also the time when there is the greatest overlap in the feeding sites of blue and great tits. It is probable that fighting for food does not pay off during the period May to August but the reason for this is not certain. Food could be both more abundant and less defendable at this time than in the winter, This would mean that if competition occurs at this time of year it is scramble competition. The low frequency of attacks and low rate of interspecific attacks during the summer does not necessarily

Table 4.3. Supplanting attacks by blue and great tits observed under natural conditions. Data from Hinde (1952). GT is great tit and BT is blue tit.

	GT	BT	TOTAL
GT	333	32	365
BT	27	214	241
TOTAL	360	246	606

2 x 2 contingency $X_c^2 = 382.2$

imply that there is no competition for food, or even that food is not a limiting resource during the breeding season.

Garnett (1976) argued that interference competition might be important during the post-fledging period. In a group of captive young great tits (10 - 40 days after fledging) he found that a dominance hierarchy developed with the older, larger young most dominant. If similar dominance hierarchies form in the wild amongst young tits, then intraspecific and possibly interspecific interference competition might have a significant effect on survival. This would be especially so because the post-fledging period, July - August, is a time of key-factor mortality (in the sense of Varley, et al 1973) for great tits (Krebs 1970, Webber 1975). However, such hierarchies, and the aggressive period preceeding their formation, have not been observed in the wild, either within or between species. Again, the caged situation probably presents an unnatural picture of the natural situation because resources are concentrated in a very limited space.

Food and feeding overlap during the breeding season

Tinbergen (1960) studied the overlap in the nestling diets of blue and great tits in Dutch pine woods. He compared the diets of the two species in a table that lists about 75 percent of all items brought to the nests. I will assume that the remaining 25 percent were probably similar to the 75 percent recorded. (The observer at the hide may not have got a good look at them.) The overlap in the items reported was $\alpha = 0.98$, an extremely high

overlap.

Betts (1955) compared the nestling diets of blue and great tits in a deciduous woodland, the Forest of Dean, Gloucestershire. The overlap between the diets of the two species was very low, but it has little meaning because the blue tit brood was sampled late in the season and the great tit brood early in the season.

I recorded the food items brought to the nests of blue and great tits. Camera boxes were set up at one blue tit and one great tit nest in each of two years. In both years the prey items were identified over a 24-hour period beginning at 1030 h 3 June 1978 and 1530 h 3 June 1979. The ages of the blue tit and great tit broods were 11 and 6 days in 1978 and 8 and 5 days in 1979. In both years the distance between nests of the two species was less than 100m and all nests were in oak mixed woodland bordering old field.

Table 4.4 lists the individual items that were brought to the great tit and blue tit nestlings. In both years there was a high overlap in the diets of the two species, $\alpha = 0.80$ in 1979 and $\alpha = 0.81$ in 1978. These overlap coefficients were calculated conservatively by assuming that all unidentified items were different. In fact, there were few enough unidentified items that their treatment makes little difference in the calculated overlap coefficients.

There appear to be several consistent differences between the two species in the two years. For example, great tits tended to take proportionately more Phigalia

Table 4.4. Prey items brought to a brood of blue tits and a brood of great tits in two different years. Overlap was calculated by counting all unidentified items as being different for the two species. Diversity was calculated using only the identified categories.

	1979		1978	
	Blue Tit	Great Tit	Blue Tit	Great Tit
Lepidoptera larvae				
Amphipyra pyrimidea	20	3	21	12
Brachionycha sphinx	2	5	9	16
Allophyes oxyacanthae	5	2	1	0
Orthosia stabilis	16	8	21	10
Hydriomena furcata	9	1	1	0
Griposia aprilina	0	0	1	12
Eupsilia transversa	0	0	1	4
Oporinia dilutata	179	124	125	92
Operophtera brumata	100	16	14	5
Erannis defoliaria	18	6	20	19
Phigalia pilosaria	12	76	25	32
Colotois pennaria	5	15	5	2
Tortrix viridana	6	3	99	15
Unidentified	36	23	16	23
Tortricoid pupae	3	5	3	0
Tipulidae	1	3	1	26
Bibionidae	9	3	1	0
Unidentified Diptera	3	3	1	0
Spiders and egg cocoons	49	39	39	26
Blue tit only	1	0	15	0
Great tit only	0	19	0	5
Unidentified	2	6	14	12
TOTAL	476	360	432	311
DIVERSITY (H)	0.80	0.84	0.89	0.96
OVERLAP (within year)	0.80		0.81	

pilosaria in both years while blue tits took more Operophtera brumata. If there are consistent differences between the two species then there should be a significant trend toward taking the same prey items in the two years of the study. Because the abundance of the various prey species in the environment may change between years, the relative proportions of each prey species should be compared between years. This was done for all prey categories with at least 10 records in both 1978 and 1979 (Figure 4.5). The correlation between the two years ($r = 0.76$, $P < 0.025$) shows that the differences between the two species were significant and probably reflect some consistent differences in foraging. However, despite the consistent differences there was a substantial overlap in prey species and most prey were taken by both blue tits and great tits.

The differences between the diets of the two tit species did not show any clear differences in feeding habitat. Tortrix viridana was associated almost exclusively with oak and was used most by blue tits. However, Phigalia pilosaria is also associated with oaks in Wytham (Royama 1970) and was taken largely by great tits.

There appeared to be no difference in the niche width of the two species in terms of nestling foods. The Shannon (1948) index of diversity, $H = -\sum_i p_i \log p_i$, was calculated for each species and year in Table 4.4 using all identified categories of prey items. Contrary to the suggestion of Dhondt (1977) the blue tits had, if anything, a somewhat less diverse diet as compared to the

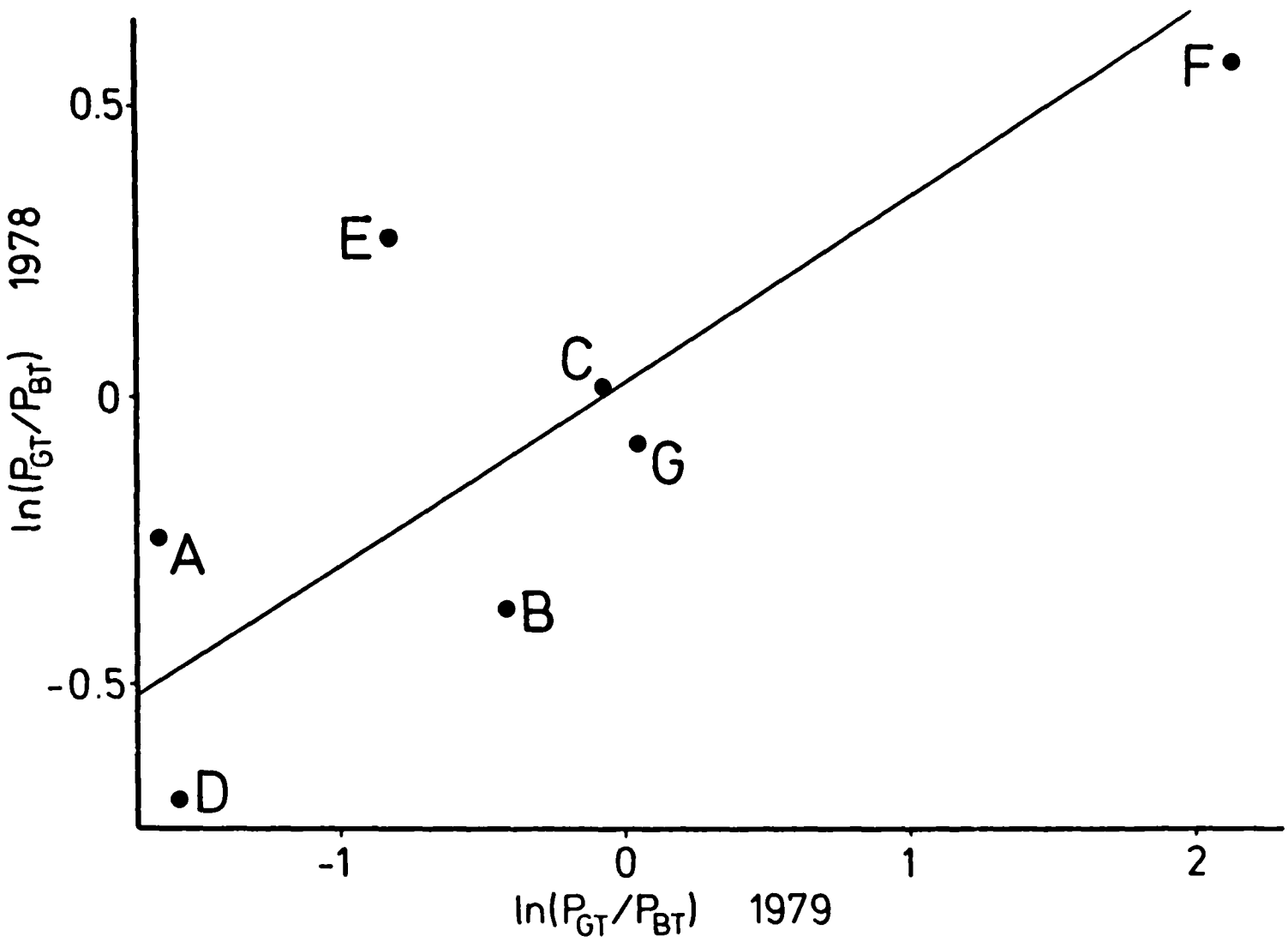


Figure 4.5 Comparison of prey selection by blue and great tits in 1978 and 1979. P_{GT} and P_{BT} are the proportions of each prey type in the diets of great and blue tits. The line is the major axis. The correlation coefficient is significant ($r = 0.76$, $P < 0.025$). The prey items are A. Amphipyra pyrimidea, B. Orthosia stabilis, C. Oporinia dilutata, D. Operophtera brumata, F. Phigalia pilosaria, and G. Spiders and egg cocoons. Only prey represented by at least 10 items in both 1978 and 1979 are included.

great tits.

Besides eating different foods, blue and great tits might avoid competition by either feeding in different places or feeding at different times. The overlapping territories and high feeding site overlap in breeding blue and great tits shows that separation by place of feeding is unlikely.

It is possible that the two species feed more actively at different times of day. To test the possibility of temporal separation I compared the times that prey items were brought to the nest. Feeding rate was expressed as the number of feeding visits per bird per hour. Table 4.5 shows the effect of various factors on the feeding rates of the birds. An analysis of variance was used to determine which effects were significant (Table 4.6). The interaction of species and time of day was not significant ($F_{15,83} = 1.10$) showing that the two species probably do not feed their young more actively at different times of day. Both species had similar diurnal rhythms with peaks of feeding activity in the early morning (Figure 4.6).

Food depletion

Several studies have attempted to measure the effect of tit predation on the food supply during the nesting season. Betts (1955) worked in a deciduous woodland, the Forest of Dean, and estimated that tits took between 1 and 5 percent of the total insect food supply. Her analysis gives a minimum figure for the effect of depletion on the tits. Some insects are not suitable for tits and

Table 4.5. The effects of sex, species, and time of day on the number of feeding visits per bird per hour at nest boxes. GT is great tit and BT is blue tit.

Grand Mean 12.33 feeding visits per bird per hour.

Sex	Male	Female
	13.30	11.36

Time	0500h	0600h	0700h	0800h	0900h	1000h	1100h	1200h
Species								
GT	10.22	16.72	13.22	21.72	18.72	9.95	11.70	11.70
BT	12.05	17.55	13.30	16.80	16.80	14.55	10.30	15.30
Mean	11.14	17.13	13.26	19.26	17.76	12.25	11.00	13.50

Time	1300h	1400h	1500h	1600h	1700h	1800h	1900h	2000h
Species								
GT	8.70	11.20	10.20	11.95	11.45	11.70	13.20	4.95
BT	10.80	9.30	11.55	9.80	7.05	13.05	5.80	13.30
Mean	9.75	10.25	10.88	10.88	9.25	12.38	9.50	9.13

Table 4-6. Analysis of variance of the feeding rates of tits. D.F. is degrees of freedom. Interaction is shown by a hyphen between factors, eg. 'species-time'.

Source of Variation	D.F.	Percent Sum of Squares	Mean Square	F-Ratio
Year Stratum	1	11.43	451.39	16.36
Species Stratum	1	0.29	11.50	0.41
Year-Species Stratum	1	0.12	4.64	0.17
Year-Species-Units Stratum				
Sex	1	3.03	119.46	4.33*
Time	15	30.19	79.45	2.88**
Species-Time	15	11.56	30.41	1.10ns
Residual	83[a]	58.00	27.59	
Total	114[a]	102.77	35.59	
Grand Total	117[a]	114.61		

[a] Time of 10 observations missing because watch stopped. Treated as missing data.

* $P < 0.05$

** $P < 0.001$

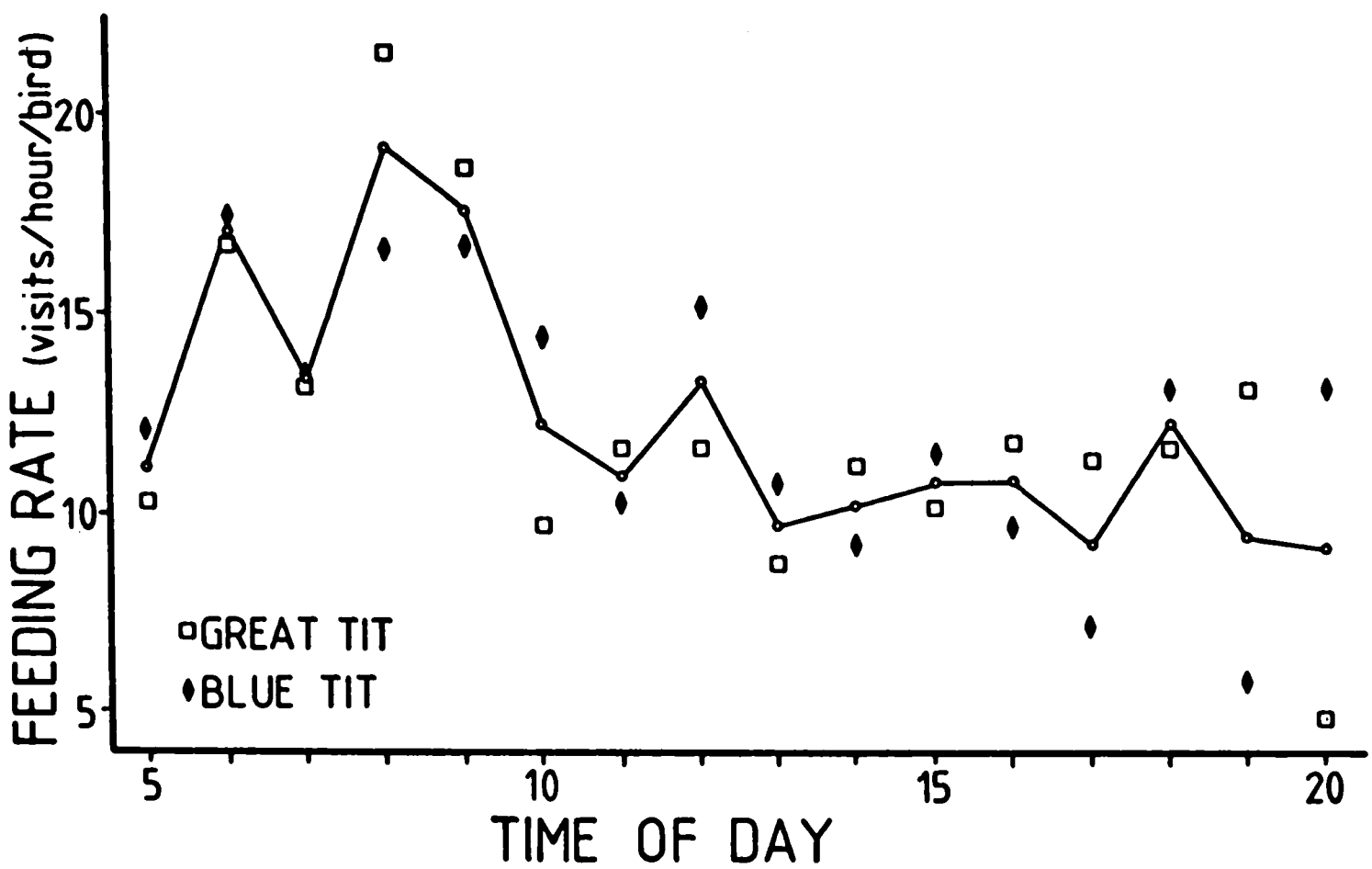


Figure 4.6 Effect of time of day on the feeding rates of a great tit and a blue tit pair in both 1978 and 1979 (i.e., four pairs). Time of day is in hours (5 = 0500h, etc).

others may not be available to them. Also, unlike Wytham, the tits in the Forest of Dean shared the woods with the more numerous pied flycatchers.

Tinbergen (1949) estimated the depletion of individual prey species from pine woodlands in Holland. During the nestling period preferred prey items were depleted by up to 37 percent. This figure is probably high for deciduous woodlands but it highlights the impact of tits on selected or preferred prey items. The tits in Wytham probably experience a total depletion between the estimates of Betts and Tinbergen although there is probably considerable variation between years.

CONCLUSIONS

Blue and great tits change their foraging sites with season and overlap most during the breeding season. The meaning of the high overlap is confounded by the great abundance of prey items during the breeding season. During the winter tits spend most of the short days feeding. There are certainly more aggressive encounters during the winter than during the summer, and a greater proportion of these encounters are interspecific despite the greater difference in foraging sites in winter compared with summer. This is not necessarily a result of just a food shortage. It may be because in winter tits forage more in flocks and these are often mixed species flocks. Also, winter foods such as beech nuts may be easier to steal and the reward from interference competition may be greater (Garnett 1976). Conversely, the decreased

aggression and increased feeding overlap during the breeding season does not show that there is no competition for food.

The high overlaps in prey species brought to the nest and feeding sites during the nesting season show that there is the potential for competition during the breeding season. The breeding season is probably the time when most density dependent control of the great tit population occurs (Krebs 1970, Webber 1975). During the breeding season intraspecific territory size will vary with intraspecific density so a high density of great tits will lead to smaller great tit territories. However, because great tits and blue tits do not maintain interspecific territories, a greater density of one species will create more scramble competition for the other. Thus, if scramble competition is significant, reproductive success ought to depend on both intra- and interspecific breeding density. The following chapters examine various aspects of density dependent effects on the two populations.

CHAPTER 5

Breeding Density, First Egg Date, and Dispersal Distance

It is virtually axiomatic that competition should increase at higher densities of competitors. Thus, when a particular feature of the breeding biology of a species is density dependent it may be that competition is the causal agent. There are obvious tautological difficulties in merely equating competition and density. For example, to say that territories are smaller at higher densities because of increased competition may well be true, but the separation of cause and effect is clearly impossible without further information. It is necessary to make a quantifiable prediction about the effect of competition that is at least falsifiable.

In this chapter I will examine the effects of breeding density on the timing of breeding and on natal dispersal. The natal dispersal distance of great tits has been related to the breeding density of great tits (Greenwood, et al 1979). I shall examine the additional effect of blue tit density on great tit natal dispersal.

The effect of interspecific density on the timing of breeding for blue tits and great tits has not been examined before. The problem with examining the effects of density is that the date of clutch initiation (first egg date) is primarily dependent on spring temperatures.

Tollanaar (1922), Kluijver (1951, 1952) and Perrins (1965) have shown that great tits begin laying eggs at an earlier date in years with warm spring temperatures.

Perrins found that the sum of the mean daily temperatures from 1 March to 20 April was negatively correlated with the mean first egg date of great tits breeding in Marley Wood. Kluijver (1952) found a similar correlation based on the period 16 March to 20 April for great tits breeding in Holland. Both Perrins and Kluijver recognized the shortcomings of choosing a fixed period over which the spring temperatures were measured. After a very mild winter tits may begin laying at the beginning of April. Egg formation begins about four days before the first egg is laid (Kluijver 1951). Thus, April temperatures may be of little importance in early years. Conversely, there are years when the first egg may not be laid until late April and the mean first egg date has been as late as 10 May. Nevertheless, the choice of a fixed period allows a simple model that fits the data well. One reason for its success is that temperatures tended to be correlated over fairly long periods of time.

With the strong effect of temperature on first egg dates, a multivariate approach is needed to study the effect of density. If breeding densities affect the first egg dates, they should explain residual variation not explained by spring temperatures alone. More over, as shown in Chapter 2, there may be an effect of spring temperatures on breeding numbers. If breeding numbers are correlated with spring temperatures, there might be a spurious correlation between density and first egg dates. This is a further reason for including spring temperatures in a model for the effect of density on first egg date. This reason-

ing is behind the multiple regression approach to examining first egg dates.

METHODS

First egg dates

First egg dates were measured in days, starting on 1 April (eg 20 April = 20, 15 May = 45). In calculating the first egg date for a nest it was assumed that one egg was laid each morning on successive days. Thus, a nest with five eggs on 4 May was estimated to have a first egg date of 30. This estimation is occasionally slightly inaccurate, especially in the case of blue tits. Blue tits (but very rarely great tits) may stop laying for several days if the weather is cold or rainy, and then resume laying. Thus, the estimated first egg dates for blue tits may be slightly greater than the true first egg dates.

Annual mean first egg dates are calculated on the basis of each first egg date excluding late or repeat nests (as defined below). One problem with calculating a mean is that it will be affected by the extent of renesting. Thus, if the level of predation was high in one year, the mean first egg date would be later than if the predation had not occurred, unless repeats are not counted. Renesting may cause the distribution of first egg dates to be highly non-normal and perhaps bimodal.

I used a somewhat arbitrary criterion for selecting those first egg dates that were included in the annual means. I used those dates that were within 14 days of the last date in the first 10% of first egg dates. For example, given the first egg dates: 17,19,20,21,21;23,23,23,24,24,

25,25,27,29,31,34,36,39,48; the date '19' was the last of the first 10% so every date up to and including '33' would be included. In the example the range of dates included was 17 to 31, the mean was 23.47, the standard deviation was 3.70, and the sample size was 15. Based on known cases of renesting, this seems a reasonable procedure for estimating the mean date of first nesting attempts for blue and great tits.

Spring temperatures were based on data from the Radcliffe Observatory, Oxford. Minimum and maximum daily temperatures were recorded. For both March and April the mean minimum and maximum temperatures were calculated for each year. These means were used as variates to predict the mean first egg dates.

I used first egg data from Bean Wood for the years 1962 to 1978. Bean Wood was chosen because of the very high densities of both blue and great tits. A section of high breeding density seemed the most likely place to detect an effect of density on first egg date.

Dispersal distances

I used published data for great tit natal dispersal distances (Greenwood, et al 1979). These distances were based on the distance from the nest box from which a bird fledged to the nest box at which it bred the following year. Greenwood et al also estimated the number of territories crossed from the natal site to the breeding site, based on the mean breeding density of great tits in each year. Holding the dispersal distance constant, there would be a doubling of the number of territories crossed for each

four-fold increase in breeding density. That is; where T = mean number of territories crossed, d = mean dispersal distance, D = breeding density, and k is a constant; for any year t, $T_t = k\ D_t\ d_t^2$. In my analysis I shall be trying to show an association between dispersal distance (d) and density (D), as well as the effect of the density of congeners. If there is no correlation between D and d, then some correlation between d and T might be expected because of the high correlation between d and d^2, i.e. there is a problem of autocorrelation. It is really only fair to test either distance or territories crossed as dependent variables predicted by breeding density. Preferably, distance should be tested as there is less reason to suspect that it should be correlated with density. Still, if density fails to predict distance, it may be useful to consider the number of territories crossed for heuristic purposes. Although the significance of intraspecific density should be constrained to the single test, there is no reason not to make both tests for other independent variables. These could include interspecific density, especially if there was a low correlation between the inter- and intraspecific densities.

RESULTS AND DISCUSSION

First egg dates

The first egg dates for blue and great tits in Bean Wood are given in Table 5.1. Blue and great tit densities are in Tables 2.5 and 2.6. Spring temperatures are in Table 5.2.

Multiple regression analysis was used to determine the

Table 5.1. Mean first egg dates for blue and great tits in Bean Wood. Very late clutches were removed from the samples (see methods). Dates are calculated from 1 April (e.g. 1 April = 1, 1 May = 31, etc.).

	GREAT TIT		BLUE TIT	
Year	Date	± sd	Date	± sd
1961	19.84	4.34	16.04	3.63
1962	31.85	2.23	30.61	4.43
1963	28.69	2.50	27.81	3.87
1964	31.91	2.75	28.10	3.32
1965	29.80	5.50	22.00	4.45
1966	31.46	3.80	26.31	4.11
1967	26.71	6.82	17.96	3.63
1968	25.60	4.90	23.91	2.38
1969	30.19	6.38	31.31	4.85
1970	35.36	3.03	35.72	2.70
1971	35.05	4.81	29.89	3.19
1972	25.00	4.59	18.19	4.75
1973	31.43	3.76	21.45	3.80
1974	28.53	4.81	18.51	4.05
1975	33.93	4.23	30.23	4.48
1976	28.00	4.40	23.32	3.42
1977	35.83	4.58	35.15	6.51
1978	39.04	3.22	34.86	3.96

Table 5.2 . Means of March and April daily minimum and maximum temperatures for 1961-1978. Temperature is in degrees Fahrenheit (^{o}F).

Year	March minimum	March maximum	April minimum	April maximum
1961	38.6	56.5	44.6	47.9
1962	30.8	45.1	40.1	53.6
1963	37.4	49.7	42.2	55.8
1964	35.8	44.9	42.0	54.7
1965	35.2	50.2	40.1	55.5
1966	37.8	51.1	41.0	52.1
1967	39.6	52.1	40.6	53.6
1968	38.5	51.1	39.9	55.3
1969	34.1	45.0	38.6	55.6
1970	33.2	45.7	40.0	52.3
1971	36.0	47.7	39.8	53.5
1972	37.0	53.2	41.7	53.8
1973	35.8	51.8	39.6	53.6
1974	36.1	48.7	38.8	55.4
1975	36.6	46.0	41.5	55.1
1976	35.1	47.9	39.6	55.2
1977	39.7	50.8	38.9	53.2
1978	38.0	51.4	37.9	50.4

possible effects of spring temperatures and blue and great tit densities. The results for blue tits are in Table 5.3. The mean blue tit first egg dates were apparently independent of breeding density, although the simple correlation with density was positive (Table 5.4). There was a high correlation between spring mean maximum temperatures and first egg dates. Even the simple correlations (Table 5.4) between first egg dates and mean minimums were quite low, despite the reasonable correlation between March mean minima and maxima. April mean minima and maxima were not highly correlated.

Great tit first egg date was affected by both blue and great tit densities as well as by spring temperatures (Table 5.5). At higher breeding densities of tits the first egg dates of great tits were retarded. For great tits this could be caused partly by the increased number of first year females which tend to breed one to three days later than older females (Kluijver 1951, Perrins 1965). However, this is not enough to explain the regression coefficient of 3.39 days delay for every increase of one great tit pair per hectare. Presumably, a further factor, probably to do with competition, is responsible for the intraspecific density-dependent delay. Moreover, the effect of blue tit density is difficult to explain without suggesting that some form of competition was responsible for the delay in breeding. This is especially true because of the low correlation between blue and great tit numbers (Table 5.4).

A delay in first egg date is not bad <u>per se</u>, but first

Table 5.3. Factors associated with the mean first egg dates of blue tits in Bean Wood from 1962 - 1978. MH and AH are the mean March and April daily maximum temperatures in degrees Fahrenheit (^{o}F).

Blue tit first egg date (55.5% of variance explained)

Variate	Coefficient	t-test	P_t
Constant	220.15	5.06	0.001
MH	-1.37	3.90	0.001
AH	-2.34	3.55	0.001

Table 5.4. Correlation matrix of factors associated with blue tit and great tit mean first egg dates in Bean Wood from 1962 to 1978. ML, MH, AL, and AH are the mean March minimum, March maximum, April minimum, and April maximum. GT and BT are the breeding densities of great and blue tits. GTE and BTE are the mean first egg dates of great and blue tits. A+MH is the sum of the April and March mean maximum temperatures. G+BT is the sum of blue and great tit densities. (n.b. $P(r_{15} > 0.48) < 0.05$, $P(r_{15} > 0.41) < 0.10$, 2-tailed)

	ML	MH	AL	AH	A+MH	GT	BT	G+BT	GTE
MH	.71								
AL	.06	-.04							
AH	-.04	-.27	.30						
A+MH	.64	.86	.12	.27					
GT	.08	-.21	.25	.01	-.21				
BT	.35	.01	-.50	-.20	-.10	.12			
G+BT	.33	-.10	-.29	-.16	-.18	.58	.88		
GTE	-.09	-.28	-.36	-.64	-.62	.42	.47	.58	
BTE	-.24	-.51	-.23	-.43	-.74	.27	.32	.39	.82

Table 5.5. Factors associated with mean first egg dates of great tits in Bean Wood from 1962 to 1978. MH and AH are mean March and April daily maximum temperatures in degrees Fahrenheit (^{o}F). GT and BT are the densities of blue and great tits in pairs per hectare.

Great tit first egg date (76.1% of variance explained)

Variate	Coefficient	t-test	P_t	%V	P_V
Constant	147.06	6.44	0.001		
MH	-0.558	3.11	0.005	57.0	0.001
AH	-1.79	5.32	0.001		
GT	3.39	2.47	0.025	11.2	0.025
BT	1.77	2.30	0.025	7.9	0.025

egg dates are related to a number of other factors. The clutch sizes are smaller for tits laying later in the season (Kluijver 1951, Perrins 1965, also see Chapter 6). Further, the fledging weights of great tits decrease as first egg date increases (Chapter 6). Hence, first egg date is related to the breeding success of a pair, probably because of the greater abundance of insect food earlier in the nestling period. Whatever the reason, it would seem that the majority of birds would do better to initiate their clutches sooner rather than later than they do.

A caveat should be entered here. There is a bit of circularity to the argument that most birds should lay earlier because those that do lay earlier do better. It may be that good pairs on good territories can afford to breed earlier and that each pair actually does a good job of estimating its optimum starting date. At high densities of competitors it may actually be advantageous to delay breeding in order to maximize breeding success. Thus, breeding densities in the prelaying period may act as a proximate factor in determining first egg dates of tits. The ultimate cause may be the effect of competition on the availability and predictability of food later in the season. Perrins (1970) made a similar argument for the ultimate and proximate effects of spring temperatures on first egg dates.

Nevertheless, at high densities there is probably even greater pressure to breed early as compared with low densities. There should be a better food supply for early

broods. Young that fledge early will have less competition during the critical period just after fledging. Early fledging young should be more likely to secure a breeding territory near their natal territory. At high densities, increased competition during the pre-laying period probably results in an increased expenditure on territorial defense, nest site acquisition, and time spent foraging. Presumably, these costs would result in a delay of breeding.

Dispersal distances

Greenwood et al (1979) showed that natal dispersal distance for females was negatively related with great tit breeding density and for males the number of territories crossed was negatively related to the great tit density. I was interested in whether blue tit density also affected the dispersal of great tits.

The effect of blue tit density on the natal dispersal distance of great tit females was positive, i.e., females moved further in years with a high density of blue tits (Table 5.6). The reason for this is not clear because the exact timing of the dispersal is not known. It might be, for example, that the greater competition for food with blue tits in the post-fledging period caused the female great tits to move greater distances; yet higher densities of great tits would mean that a mate was closer to hand and therefore long movements were not necessary.

The result for male dispersal distance of great tits showed just the opposite trend to that for females. Males moved shorter distances in years with large numbers of blue tits, and also traversed fewer territories (Table 5.6).

Table 5.6 Relationship between natal dispersal distances of great tits and breeding densities of blue and great tits in Wytham Woods (1964-1975). GT and BT are great tit and blue tit densities in pairs per hectare for all of Wytham. DM and DF are the median dispersal distances (m) of male and female great tits. DMT is the median number of territories crossed by males. A correlation matrix is given after the regression analyses. Data from Greenwood et al (1979).

Dispersal distance (DF) of females (68.1% of variance expl.)

	Coefficient	t-test	P_t	%V	P_V
Constant	1076.8	4.72	0.001		
GT	-655.7	3.58	0.005	53.2	0.005
BT	267.4	2.38	0.05	14.9	0.05

Dispersal distance (DM) of males (26.1% of variance expl.)

	Coefficient	t-test	P_t
Constant	990.6	4.92	0.001
BT	-356.8	2.21	0.10

Dispersal distance (DMT) of males (27.1% of variance expl.)

	Coefficient	t-test	P_t
Constant	8.63	4.73	0.001
BT	-3.30	2.25	0.05

BT	-.29			
DM	.22	-.57		
DF	-.76	.61	-.39	
DMT	.49	-.58	.95	-.56
	GT	BT	DM	DF

Again, the causes of this are far from obvious. It may be that the greater competition from blue tits meant that only those males near their natal territories were in a strong enough position to defend a territory.

There are just too many forces at work to make a clear picture based on a simple analysis of 12 years of data. For example, great tits in the low nest box density sections at the centre of the Woods (Extra, Common Piece and Broad Oak) may experience a relative competitive release during years of high blue tit populations. Whatever the causes involved, the analysis does show that blue tit density had a significant correlation with the dispersal distance of great tits. Such a relationship is likely to reflect a significant effect on the survival and reproduction of great tits in their first year.

CONCLUSIONS

Blue tit density had an effect on both the first egg date and natal dispersal distances of great tits. In the absence of any other explanation it seems reasonable to attribute the cause to some form of competition between the two species. If this explanation is vague, it is probably more honest than the multitude of plausible explanations. Either scramble competition or interference competition could result in the observed effects, although in the case of blue tits affecting great tits, it would seem that scramble competition, probably for food, is the most likely. This certainly appears to be the explanation for the negative effect of blue tit density on great tit fledging weight which is discussed in Chapters 6 and 7.

The model for first egg date was sufficient to show the effect of blue tit density on great tits. There are other ways of modelling first egg dates. For example, rather than take the average temperature over a fixed period, the date on which a moving average of daily temperatures reached a certain threshold could be used instead. However, if the birds are using a threshold temperature (or a proximate factor related to a threshold temperature), the threshold is probably higher in early April than in early May. This possible interaction between date and threshold temperature would result in a more complex model that would require a long run of data. However, such a model might further reduce the variation caused by weather so that the possible effects of density and other factors might be more sensitively assessed.

CHAPTER 6

Clutch Size and Fledging Weight

The reproductive success of an animal can be measured in terms of the number of offspring it produces which survive to breed. Birds, such as the tits in Wytham, often rear only one brood per year. The clutch size of such birds will determine their upper limit of breeding success in any year. Leaving aside the problem of parental survival, a bird should rear as many surviving offspring as possible (Charnov and Krebs 1974). This means that clutch size or number of fledglings is not the only criterion for success. The survival of each individual offspring must also be considered. Thus, a bird should try to maximize the product of the number of offspring and mean probability of survival of the offspring. Various routes toward achieving this goal have evolved in species in which parental care is important. In predictable environments the birds may try to anticipate the optimum clutch size.

Tits appear to follow the latter strategy. They do not simply lay a large clutch and later reduce the number of young. Experiments in which eggs were removed from or added to the natural clutches of blue and great tits showed that the birds attempted to achieve a certain clutch size (Winkel 1970; Euan Dunn, personal communication), rather than lay a number of eggs constrained only by a physiological upper limit. Experiments by Källander (1974) and John Krebs (personal communication) indicated that the onset of breeding is advanced when artificial food is supplied,

but that clutch size is not increased. The apparent conclusion is that the tits make an assessment of their environment and adjust their clutch size according to their expectations of future conditions. Still, for some individuals and in some years, it may be physiologically impossible to achieve the clutch size necessary for the production of the maximum number of surviving young.

If clutch size is primarily determined as a behavioural response to the environment, then the crucial period for the limitation on the number of surviving offspring must occur after egg laying, perhaps during the nestling period. Perrins (1965) has shown that the survival of young great tits is related to their weight just prior to fledging. That is, a large brood of light young may not represent as much parental success as a smaller brood of heavier young. It would appear that tits must 'estimate' the clutch size which will maximize their probability of success and then proceed to make the most of the situation during the nestling period.

Both density dependent and density independent factors will determine the optimum clutch size for a bird. The density of competitors will determine the amount of food available during the nestling period. The local density of conspecifics can be assessed by the size of the breeding territory at the time of egg laying. Local density could serve as an index of the amount of competition for food that might occur during the nestling period. The assessment of the breeding density of congeners might not be quite so easy for the blue and great tits because they do

not maintain interspecific territories.

Density independent factors affecting clutch size would include the quality of the habitat and the timing of clutch initiation. In poor habitats (or possibly poor years) tits will have to work hard to rear even a few young. Clutches initiated late in the year will not have as much insect food for nestlings as earlier clutches. Finally, intrinsic factors may affect clutch size, for example, a first year female may not be able to rear as many young as a more experienced adult female.

This chapter analyses a number of the factors that could potentially affect clutch size and fledging weight. The high intercorrelation of a number of the independent variables associated with clutch size and fledging weight make firm statements about cause and effect almost impossible. However, a variety of independent factors are implicated by their predictive association with clutch size and fledging weight.

METHODS

Clutch size

Potentially, a number of factors might affect great and blue tit clutch size. I used multiple regression to examine the effects of first egg date*, first egg date corrected for within year mean*, female age (first year, adult or unknown), section of the Woods, great tit density, blue tit density and the beech crop in the previous autumn. Variates with asterisks (*) were treated as polynomials of up to a quartic (i.e. fourth power as in X^4) term. Each breeding attempt was treated as a separate case. Thus,

clutch size, the dependent variable, was not a continuous variable but an integer variable. The first egg date was counted in days from 31 March, e.g., 1 = 1April, 31 = 1 May, etc. The corrected first egg date was the first egg date minus the mean first egg date for the year. The mean first egg date was calculated from a truncated set of first egg dates in order to eliminate possible second nests (see Chapter 5). The annual density of blue and great tits was measured in pairs per hectare within each section of the Wood. For blue tits data from three sections of the Wood were analysed for 1964-1978. These were Marley Wood, Marley Plantation, and Bean Wood. For great tits there were also three sections, Marley (Marley Wood plus Marley Plantation), Bean Wood and Broad Oak, with data from 1961 to 1977. Only breeding attempts which eventually resulted in fledged young were included in the analysis.

The regression for factors affecting clutch size was first run as a step-up multiple regression to discover which variables could account for variance in clutch size. Certain factors were only included as a group, i.e., the group was included as a set if its inclusion resulted in a significant reduction in the error mean square for the regression. These groups included female age, section of the Wood, and great tit or blue tit density by section of the Wood. The analyses were then re-run with the additional grouping of all significant terms of each polynomial factor to determine the amount of variance explained by each factor by adding all terms of a factor to the model at the same time.

Some alternate models were tried for great tit clutch size in which great tit and blue tit density were treated as quadratic polynomials, but clutch size was considered for only one section of the Woods in these models.

Great tit fledging weight

Only the weights of great tit nestlings have been recorded systematically in Wytham. Nestlings are weighed on their 15th day as some broods might fledge prematurely if weighed later. I shall refer to 15th-day weight as 'fledging weight' as it is the nearest approximation available.

Polynomial multiple regression was used to determine which factors were associated with mean fledging weight for 882 great tit broods over 13 years in Bean Wood, Marley, and Broad Oak. Factors included in the regression were laying date*, laying date corrected for within year mean*, clutch size*, number of young fledged*, change in brood size* (number of young fledged minus clutch size), great tit and blue tit density in each section of the Wood, female age (first year, adult, or unknown), section of the Wood (Bean Wood, Marley, or Broad Oak), and year (1961-1964, 1966, 1967, 1971-1977). Factors marked with an asterisk (*) were fitted as polynomials of up to a quartic term. The factors were eliminated by a stepdown procedure until all remaining factors made a significant contribution to the amount of variance explained. There were several levels within the factors year, section of the Wood, female age, and species density by section. It was the contribution of each of these factors, rather than the individual levels of each factor, that was the criterion for elimina-

tion.

The factor year was included as 12 dummy variables to account for year to year variations in breeding success. Because only three sections of the Wood were studied, the inclusion of year reduced the power of the model for detecting the possible contribution of breeding density in each section of the Wood. However, year to year breeding density has not been highly correlated between sections of the Woods. The polynomial terms were applied to variables unique to each nesting record. Note that the model does not account for interaction between the polynomial terms and section of the Wood.

General

The influence of some factors on clutch size or fledging weight may not be linear. To test for a more complex effect of some factors I used polynomial terms. The use of polynomials complicates the interpretation of the results because it is difficult to attach biological meaning to each term. Rather, the function defined by all the polynomial terms of a particular factor should be examined. In several instances I have graphed the polynomial relationships to help visualize what is happening.

It should be remembered that while regression provides a useful technique for predicting a dependent variate based on a set of independent variates, causal relationships should be inferred with some caution. This is especially true where there are high and complex correlations amongst the independent variables under consideration. For example, first year females tend to breed later in the season, form

a higher proportion of the breeding population in years of high density (which tend to follow good beech crops), and lay smaller clutches than older females.

RESULTS AND DISCUSSION

Clutch size - a simple analysis

Lack (1966:Table 2) published data on blue tit and great tit mean clutch sizes for Marley Wood from 1947 to 1964. He also listed the breeding numbers and mean annual first egg dates for both species. I used his data for the years 1949 to 1964 to see if density and mean first egg date could be used to predict the clutch size of the two species. I also included a dummy variable for the beech crop. The results of the analysis for blue and great tits are in Table 6.1 and a correlation matrix for the variates is in Table 6.2. The clutch size of great tits was higher in years of low great tit density and also higher in years with an early spring when great tits could begin laying earlier. The interspecific effect of blue tit numbers was not significant. Blue tit clutch size was also negatively related to the number of great tits. The simple correlation between blue tit numbers and clutch size was negative, but not significant. The partial correlation of blue tit numbers with clutch size was positive, correcting for great tit density, although this was also not significant.

It appears that great tit numbers had a strong influence on the clutch sizes of both blue and great tits. Great tit density is correlated with a number of other factors and it is worth trying to discover whether it is great tit density *per se* or other correlated factors which account

Table 6.1. Factors associated with blue tit and great tit clutch size in Marley Wood from 1949-1964. GT and BT are the densities of great and blue tit pairs per hectare. GED is great tit mean first egg date (1=1 April, 31=1 May, etc.).Probabilities are one-tailed.

Great tit clutch size (49.8% of variance explained)

	Coefficient	t-test	P_t	%V	P_V
Constant	11.79	14.18	0.001		
GT	-0.934	4.08	0.001	39.1	0.001
GED	-0.0446	2.00	0.05	10.7	0.05

Blue tit clutch size (29.9 % of variance explained)

	Coefficient	t-test	P_t	%V	P_V
Constant	11.25	25.26	0.001		
GT	-0.996	2.65	0.01	29.8	0.01
BT	0.572	1.02	n.s.	0.1	n.s.

Table 6.2. Correlation matrix of factors related to clutch size of blue and great tits in Marley Wood from 1949-1964. GT and BT are the density of great and blue tits in the Wood. GED and BED are the mean first egg dates for blue and great tits. GC and BC are the mean clutch sizes for great and blue tits. BM is a dummy variable for the beech crop (1=good, 0=poor). Data from Lack(1966; Table 2).

14 d.f.

GC	.66					
BED	.12	.01				
GED	.21	-.09	.91			
BT	-.25	-.54	-.12	-.15		
GT	-.59	-.66	-.40	-.38	.70	
BM	-.41	-.13	-.64	-.72	.24	.49
	BC	GC	BED	GED	BT	GT

for the predictive ability of great tit numbers. This is what is examined in the next two sections on blue tit and great tit clutch size.

Blue tit clutch size

The clutch size of blue tits in Marley Wood, Marley Plantation and Bean Wood was related to first egg date, corrected first egg date, the beech crop and the density of blue tits (Table 6.3). The effect of corrected first egg date can be seen in the graph of the polynomial function (Figure 6.1). Blue tits that initiated their clutches before the mean for the year had larger clutches. Clutch size declined as the season progressed. The effect of absolute first egg date was also significant and the trend was similar. Thus, a blue tit starting a clutch on the mean first egg date in a late year would be expected to have a smaller clutch than a blue tit starting its clutch on the mean first egg date of an early year. The negative correlation with the beech crop means that clutches tend to be smaller in years following a good beech crop. Finally, there is a positive relationship between the density of blue tits and clutch size. The effect of female age was not significant, although adult females did tend to have larger clutches.

The most surprising result is the very significant relationship between blue tit density and clutch size. It is difficult to give an adequate explanation for this. Possibly, the positive partial correlation resulted from the correlation of blue tit density with one or more of the other variates in the regression. Since beech mast is

Table 6.3. Factors associated with blue tit clutch size. CED is the first egg date corrected for within year mean. ED is the first egg date (1 = 1 April). BM is the beech mast index (1=good, 0=poor). BT-B, BT-C & BT-MP are the densities of blue tits in Marley Wood, Bean Wood, and Marley Plantation in pairs per hectare. B and C are dummy variables for Marley Wood and Bean Wood.

Blue tit clutch size (20.7% of variance explained)

Variate	Coefficient	t-test	P_t	%V	P_V
Constant	10,28	19.01	0.001		
CED	-0.0596	4.35	0.001		
CED^2	-0.00353	3.13	0.002	14.2	0.001
CED^3	-0.000108	3.21	0.002		
ED	-0.0591	6.05	0.001	3.0	0.001
BM	-0.0159	5.02	0.001	0.8	0.001
BT-B	0.622	1.17	ns		
BT-C	1.52	3.28	0.002	2.0	0.001
BT-MP	4.66	4.85	0.001		
B	1.88	3.33	0.002	0.7	0.001
C	1.07	1.87	0.10		

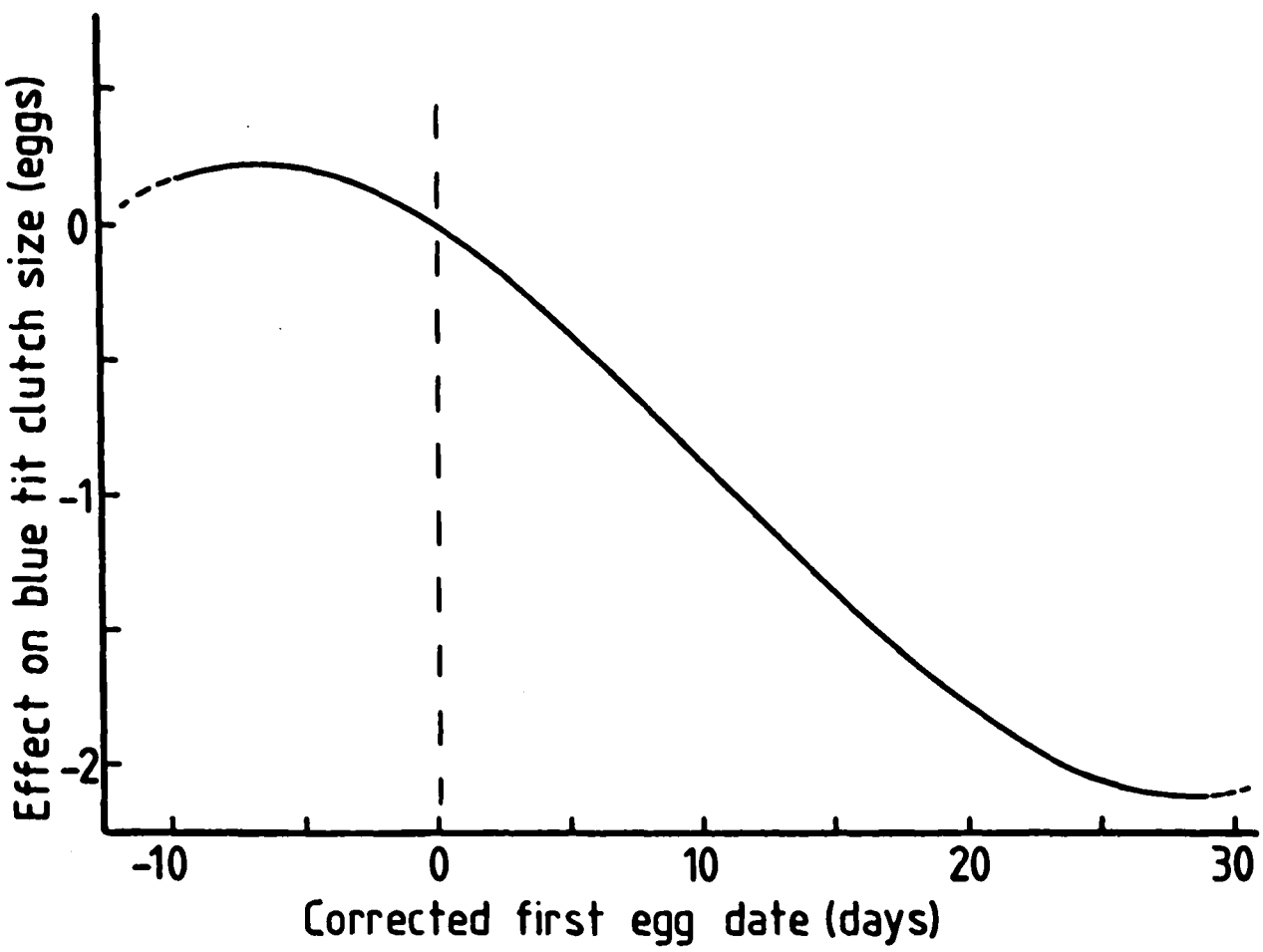


Figure 6.1 Relationship between corrected first egg date and blue tit clutch size. The curve is based on the polynomial function in Table 6.3 (p160).

known to affect blue tit density (Chapter 2), it is a likely candidate. However, dropping beech crop had no significant effect on the positive relationship between blue tit density and clutch size. Dropping beech mast did allow the inclusion of great tit density at 90% confidence. This result is not unexpected. Good beech crops are primarily correlated with large numbers of great tits (Chapter 2) as well as with large numbers of blue tits. While it would be rash to totally dismiss the effect of great tit density on blue tit clutch size, the beech crop plus other variates are adequate to explain the negative effect of great tit density. Nevertheless, dropping both blue tit first egg date and the beech crop from the regression reveals a very strong effect of great tit density on blue tit clutch size (Table 6.4). No combination of independent variables tested resulted in a negative effect of blue tit density on blue tit clutch size. The relationship was always positive and usually highly significant. Apparently, blue tits do best in years when the same conditions which caused their numbers to be high also result in the laying of larger clutches. Perhaps the blue tits take more of an 'r-strategy' approach to clutch size than the great tits. Unlike great tits, blue tit clutch size may be constrained by conditions before and during laying, whereas great tits appear to adjust clutch size according to their expectation of future competition. This suggestion is consistent with the good fledging success of blue tit broods to which I added four to ten young to natural broods of ca. eight to fourteen (Chapter 7). That is, the nestling period may not

Table 6.4. Factors associated with blue tit clutch size. Egg date and beech crop were removed from the model to determine the effect of their removal on the predictive value of the other independent variables. Symbols as in Table 6.3 except that GT stands for great tit.

Blue tit clutch size (17.9% of variance explained)

Variate	Coefficient	t-test	P_t	%V	P_V
Constant	9.05	16.35	0.001		
CED	-0.106	9.44	0.001	14.2	0.001
CED^2	-0.00334	2.91	0.005		
CED^3	-0.000977	2.85	0.005		
GT-B	-1.66	4.36	0.001	2.0	0.001
GT-C	-0.866	2.36	0.02		
GT-MP	-0.424	1.14	ns		
BT-B	-0.0307	0.06	ns	1.3	0.001
BT-C	1.23	2.51	0.02		
BT-MP	3.61	3.80	0.001		
B	2.98	4.14	0.001	0.2	0.025
C	0.888	1.23	ns		

be quite as critical for blue tits as it is for great tits. While the explanation is not wholly satisfactory, the regression results were unequivocal.

Great tit clutch size

The clutch size of great tits in Marley, Bean Wood and Broad Oak was related to the corrected first egg date, the beech crop, female age and the density of blue tits. The effect of great tit density in the multiple regression was not significant (Table 6.5). All the significant relationships are intuitively sensible. Early breeding great tits had large clutches. Adult females had larger clutches than first year females. Large numbers of blue tits depressed the clutch size of great tits. A good beech crop is related to smaller clutch sizes, probably, in part through its ability as a single dummy variable to explain residual variation caused by errors in the measurement of female age (including the unknown age category), and great tit and blue tit density.

It is surprising that the effect of great tit density was not significant. This is in part caused by the inclusion of the beech crop index in the model. The removal of beech crop decreases the variance explained by 1.0%, but the effect of great tit density becomes significant (Table 6.6). Still, the magnitude of the effect of great tit density is less than for blue tits considering the range of densities of the two species (Tables 2.5 and 2.6). Removing both the beech crop index and female age further increases the significance of great tit density, but really only in Marley (Table 6.6).

Table 6.5. Factors associated with great tit clutch size. CED is the first egg date corrected for within year mean. BM is the beech mast index (1=good, 0=poor). BT-C, BT-M, BT-O, GT-C, GT-M, and GT-O are the breeding densities of blue and great tits in Bean Wood, Marley, and Broad Oak respectively. FY-F and Ad-F are dummy variables for known first-year and adult females.

Great tit clutch size (16.0% of variance explained)

	Coefficient	t-test	P_t	%V	P_V
Constant	9.11	34.03	0.001		
CED	-0.0604	10.37	0.001	9.2	0.001
BM	-0.461	3.61	0.001	4.7	0.001
BT-C	-0.390	3.01	0.005		
BT-M	-0.293	2.61	0.01	1.0	0.005
BT-O	-0.555	2.64	0.01		
FY-F	-0.0415	0.26	ns		
Ad-F	0.306	1.92	0.10	0.9	0.005
GT-C	0.401	1.84	0.10		
GT-M	-0.0734	0.73	ns	0.2	0.20
GT-O	0.0533	0.19	ns		

Table 6.6. Factors associated with great tit clutch size. These two tables examine the effect of removing the beech mast index and then the female age from the regression in table 6.5.

Great tit clutch size (15% of variance explained)

	Coefficient	t-test	P_t	%V	P_V
Constant	9.52	39.09	0.001		
CED	-5.87	10.06	0.001	9.2	0.001
BT-C	-0.570	4.74	0.001		
BT-M	-0.486	4.91	0.001	3.5	0.001
BT-O	-0.847	4.45	0.001		
FY-F	-0.0469	0.29	ns		
Ad-F	0.349	2.18	0.05	1.5	0.001
GT-C	0.283	1.30	0.20		
GT-M	-0.250	2.81	0.005	0.8	0.01
GT-O	-0.293	1.12	ns		

Great tit clutch size (13.6% of variance explained)

	Coefficient	t-test	P_t	%V	P_V
Constant	9.77	47.49	0.001		
CED	-0.0627	10.81	0.001	9.2	0.001
BT-C	-0.587	4.85	0.001		
BT-M	-0.501	5.05	0.001	3.5	0.001
BT-O	-0.932	4.92	0.001		
GT-C	0.224	1.03	ns		
GT-M	-0.290	3.26	0.002	0.9	0.001
GT-O	-0.324	1.25	ns		

It may be better to look at great tit clutch size in a somewhat different way. I shall consider one section of the Wood at a time, use quadratic polynomials for species density, and include all factors that reduce the error mean square for the multiple regression. The result for Marley is shown in Table 6.7. Both polynomial terms for great tit density are highly significant and their removal from the regression significantly decreases the percentage variance explained (1.7%, $F_{2,574} = 6.80$, P 0.005). The effects of the polynomial terms for blue and great tit density are shown in Figure 6.2. The effect of great tit density is difficult to explain. It could be that in years of very low great tit density clutch size is low because of poor environmental conditions, such as weather, which are density independent. In very high density years clutch size could also be low because of density-dependent competition for resources.

The results for Bean Wood (Table 6.8, Figure 6.2) do not confirm the results for Marley. In fact, clutches were larger in years with both low and high densities of great tits, as compared with years with intermediate densities. It is probably too much to expect easily interpretable polynomials based on only 16 to 17 years of data for density, especially where there is a very high correlation amongst the independent variables. The analyses at least show that the effect of breeding density may not be a simple linear negative relationship with clutch size.

Table 6.7. Factors associated with the clutch size of Marley great tits. GT and BT are great tit and blue tit density in pairs per hectare. CED is first egg date corrected for within year mean. ED is the first egg date. FY-F and Ad-F are for first year and adult female.

Great tit clutch size (17.7% of variance accounted for)

Variate	Coefficient	t-test	P_t
Constant	7.73	8.80	0.001
CED	-0.0549	2.72	0.01
ED^2	-0.00275	1.39	0.20
ED^3	0.0000783	1.23	n.s.
ED^4	-0.000000591	1.08	n.s.
GT	1.79	2.62	0.01
GT^2	-0.51	3.01	0.005
BT	0.64	1.03	n.s.
BT^2	-0.25	1.60	0.20
FY-F	-0.22	0.99	n.s.
Ad-F	0.14	0.66	n.s.

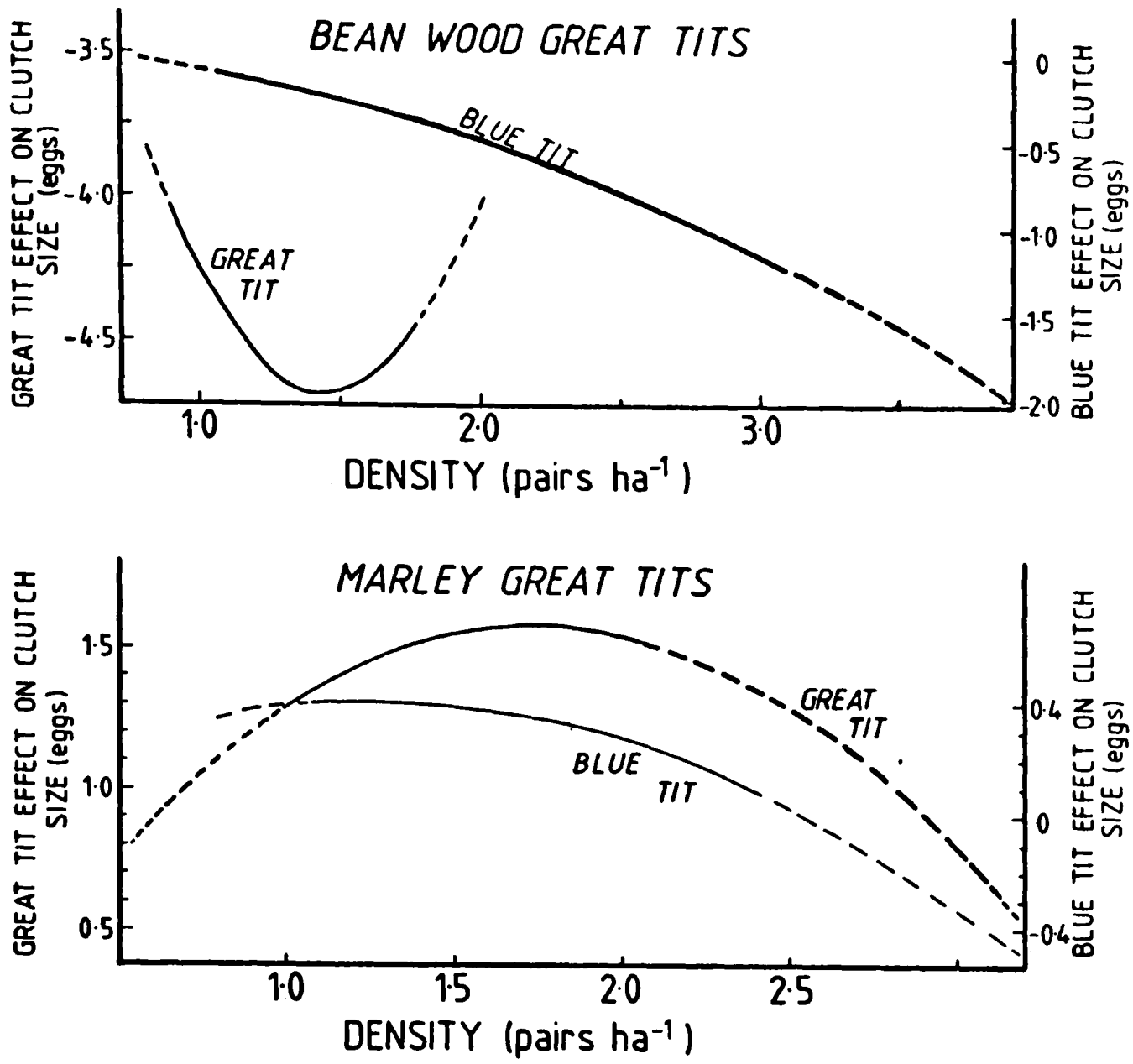


Figure 6.2 Effects of blue tit and great tit densities on the clutch sizes of Bean Wood and Marley great tits. The dashed lines connect the year of extreme low or high density to the range of all other years. Data are from 1961-1978 for Marley and 1962-1978 for Bean Wood. The curves for Marley are based on the polynomial terms in Table 6.7 (p168) and the curves for Bean Wood are from Table 6.8 (p170).

Table 6.8. Factors associated with the clutch size of Bean Wood great tits. Abbrebviations are as in Table 6.7.

Great tit clutch size (24.6% of variance accounted for)

Variate	Coefficient	t-test	P_t
Constant	13.02	4.96	0.001
ED^2	-0.00505	1.11	n.s.
ED^3	0.000258	1.61	0.20
ED^4	-0.00000292	1.98	0.05
CED^3	-0.000807	3.60	0.001
CED^4	0.0000233	3.48	0.001
GT	-6.57	2.37	0.02
GT^2	2.30	2.46	0.02
BT	0.0265	0.03	n.s.
BT^2	-0.14	0.68	n.s.
FY-F	0.25	0.60	n.s.
Ad-F	1.04	2.37	0.02

Great tit fledging weight

Five factors explain 19 percent of the variance in mean fledging weight of great tits (Table 6.9). The regression shows that great tit young in early broods tended to be heavier, young in larger broods were lighter, and young were lighter when there were more blue tits. Also, all else being equal, young in Marley broods were lighter, while Bean Wood and Broad Oak broods were more severely affected by blue tit density. Given the average densities of blue tits that have occurred in the three sections, nestling weights should be about the same in all three sections (see Figure 7.2 which is based on the regression in Table 6.9). Figure 6.3 shows the polynomial relationship between corrected first egg date and fledging weight. Broods initiated just before the annual mean first egg date tended to have the greatest mean fledging weight.

It is surprising that great tit density was not a significant factor. In fact, its inclusion in the model increased the error mean square for the regression. There are two plausible explanations. First, if it is true that great tits reduce their clutch size in years of high great tit density, the reduction may be the result of a behavioural mechanism aimed at compensating for expected intraspecific competition at the time of rearing young. If the birds have already compensated for great tit density in adjusting their brood size, it may be expected that there would be little or no correlation between fledging weight and breeding density.

There is a second plausible reason why great tit density

Table 6.9. Factors associated with the mean fledging weights of great tit broods. CED is the first egg date corrected for the within year mean. FLDG is the number of young fledged. BT-C, BT-M, and BT-O are the densities of blue tits in Bean Wood, Marley and Broad Oak. B and M are dummy variables for Bean Wood and Marley. The years 1961-1964,1966,1967,1971-1976 are dummy variables. Data come from the 882 great tit nests where young were weighed on the 15th day.

Great tit fledging weight (19.0% of variance explained)

Variate	Coefficient	t-test	P_t
Constant	21.41	40.00	0.001
$FLDG^2$	-0.00526	4.50	0.001
CED	-0.0163	1.95	0.10
CED^2	-0.00562	6.27	0.001
CED^3	0.000121	5.46	0.001
BT-C	-0.514	3.11	0.005
BT-M	-0.276	1.33	0.20
BT-O	-1.09	3.68	0.001
B	-0.0323	0.09	n.s.
M	-1.03	3.25	0.005
1961	-1.33	4.12	0.001
1962	-1.44	3.57	0.001
1963	-0.60	1.80	0.10
1964	-0.94	2.93	0.005
1966	-1.28	4.48	0.001
1967	-0.71	2.01	0.05
1971	-0.29	0.87	n.s.
1972	-0.30	0.78	n.s.
1973	-0.50	1.66	0.10
1974	-0.32	1.36	0.20
1975	-0.62	2.92	0.005
1976	-0.25	0.79	n.s.

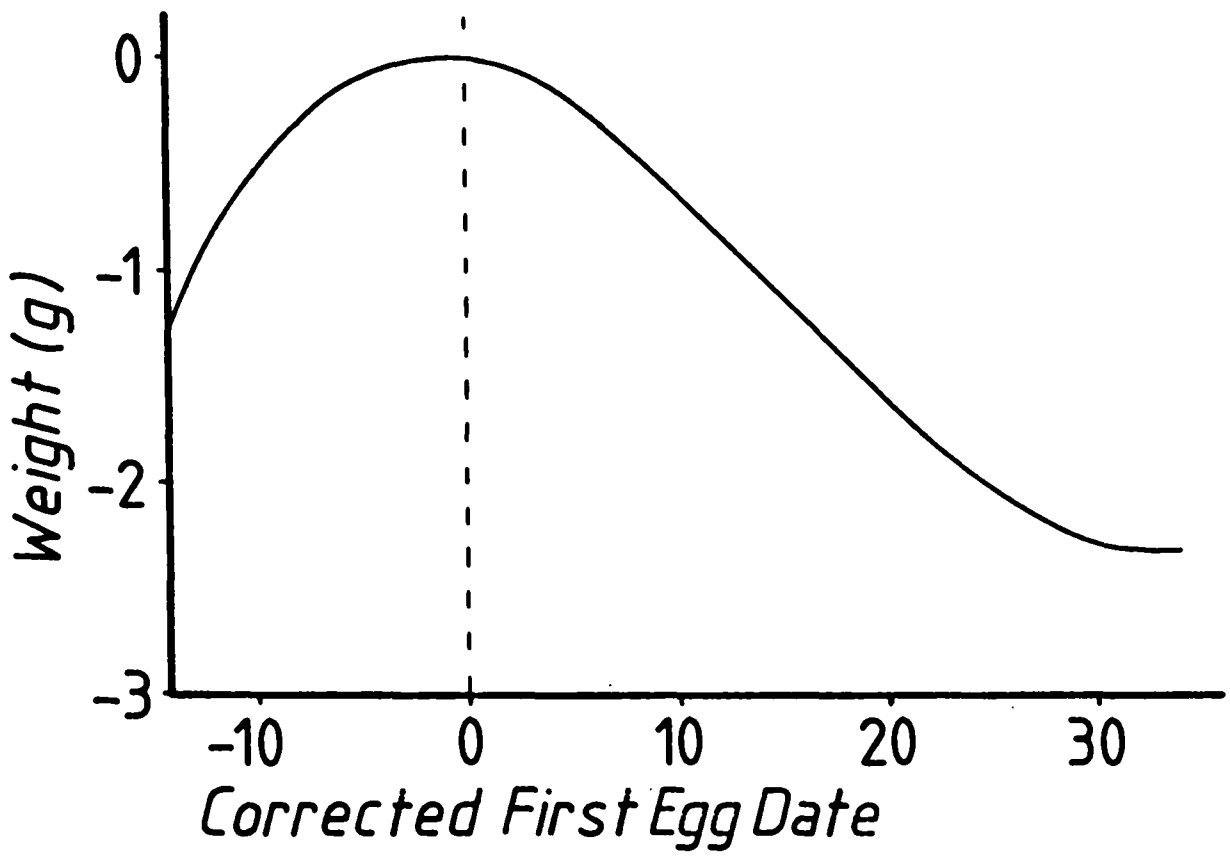


Figure 6.3 Relationship between corrected first egg date and great tit fledging weights. The curve is based on the polynomial function in Table 6.9 (p172).

was not a significant factor associated with mean 15th day weight. Krebs (1971) has shown that great tit nests tend to be evenly spaced while Green (1979) could not distinguish the spacing between blue and great tit nests from a random pattern. As shown in Chapter 3, great and blue tit territories may completely overlap, especially in high density years, with no suggestion of interspecific territoriality. Thus, during the breeding season great tits are more apt to be in direct competition for food with blue tits than with other great tits from which they are spatially separated through territoriality.

CONCLUSIONS

Both blue and great tits showed a reduction in clutch size as the breeding season progressed. There was also evidence that clutch size was lower in years with a late mean first egg date. The clutch sizes of both species were lower following years with good beech mast crops, those of great tits more so than blue tits. Clutch sizes of both species tended to be negatively correlated with tit density except that blue tit clutch size was significantly larger in years with a high density of blue tits. A positive relationship between clutch size and density is difficult to explain without suggesting a density independent environmental factor which results in both a large breeding population of blue tits and conditions favourable for large clutches. A well designed removal experiment would be needed to confirm this explanation.

Where any significant interspecific effect of density could be detected it had a negative relationship with clutch

size. For the rather simple analysis of clutch sizes in Marley from 1949 to 1964, great tit density was related to great tit clutch size. For the analyses of data from 1961 to 1978 almost the reverse was true, except that in Marley or Marley Wood the effect of great tit density was stronger than in the other sections studied. It appears, especially from the polynomial analyses of great tit density, that it may have been the several recent years of extraordinary blue tit density that are responsible for this reversal. Probably in the historically more 'normal' years the effect of blue tit density on great tit clutch size would be less marked. There certainly is no evidence to suggest whether the change in the clutch size of great tits associated with blue tit density was caused by a behavioural response or was caused by resource competition. It is also questionable whether such a situation would arise in a natural woodland where there were no nest boxes as in Wytham.

Great tit fledging weight was negatively correlated with blue tit density in at least two of the three sections of the Woods that were examined. An effect of great tit density independent of yearly environmental changes could not be detected. It may be that great tits adjusted their clutch sizes in expectation of competition from conspecifics so that interspecific density did not have a significant effect on fledging weight. The reason for the significant effect of blue tit density on great tit fledging weight may be caused, in part, by the failure on the part of the great tits to adequately adjust their clutch size earlier in the year to blue tit density. Remember. however,

that a high mean fledging weight is only half the object in maximising reproductive success. Number of young fledged is also important and the great tits may actually have the product maximised. Nevertheless, any factor that lowers both fledging weight and clutch size for great tits is a factor that lowers their breeding success.

Chapter 7 presents a test of the regression results for great tit fledging weights, by artificially manipulating blue tit density, to see if the effects on great tit fledging weights are as predicted in the model developed in this chapter.

CHAPTER 7

Effect of Experimental Manipulation of Blue Tit Density on the Reproductive Success of Great Tits

In Chapter Six I argued that competition for food during the breeding season led to reduced reproductive success for blue and great tits. I showed that the clutch size of great tits has been affected primarily by great tit density while the fledging weights of great tits have been related to blue tit density. I suggested that the great tits were able to compensate for intraspecific competition by reducing their clutch size but that they did not compensate for blue tit density. During the nestling period blue and great tits were involved in scramble competition for very similar prey items. Further, great tits were spatially separated through territoriality whereas blue tit - great tit nearest neighbor distances were not overdispersed. The net result has been that great tits must compete for food with blue tits. This chapter describes an experiment which shows that inter-specific competition significantly affects the breeding success of great tits.

The best measurement of the reproductive success of a breeding pair is the number of offspring that survive to breed. This measure is not easily made, but may be approximated by multiplying the number of young that fledge by the mean probability of survival of each individual. Perrins (1965) and Perrins and Moss (1975) have shown that the probability that a great tit nestling

will survive to breed is closely correlated with its fledging weight. Thus the reproductive success of a pair of great tits may be separated into a component associated much more with great tit density than blue tit density, i.e., the number of young, and a second component associated more with blue tit density than great tit density, the mean fledging weight of a brood.

The historical evidence (Chapter 6) indicates that blue tit density has affected great tit fledging weight and therefore breeding success. Because blue tit density has only a slight effect on great tit clutch size, most of the effect of blue tits on great tits probably occurs during the nestling period. If this is true then the removal of blue tits during the nestling period should increase the fledging weight of great tits. If the competition is primarily for food then the removal of just the blue tit nestlings should have almost the same effect as removing the adults prior to breeding or the adults plus nestlings later. It is known that blue tits increase their feeding rate as a brood increases in number (O'Connor 1973). Thus artificially increasing blue tit brood sizes in a section of the wood should depress the food supply for great tits and result in lower fledging weights for great tits. These predictions were tested in an experiment in which blue tit nestlings were removed from one section at hatching and added to broods in a second area. A third area served as a control for the two experimental areas.

METHODS

The three sections of Wytham Wood used for the experiment were the 17-hectare Bean Wood, 35-hectare Broad Oak and 40-hectare Marley (Marley Wood and Marley Plantation) (Figure 2.1). The three sections are mixed woodland dominated by oak which forms much of the canopy layer. Nest boxes in the three sections are provided at a density of about 7 per hectare; this is about twice as many boxes as are used even in years of high breeding densities of blue and great tits.

All nest boxes were checked at one week intervals starting in mid-April. Blue and great tit nests with eggs were checked daily starting just before the eggs were due to hatch. This ensured that the hatching date (defined as the day on which the first egg hatched) was known for all broods.

The great tit nests in the two experimental areas were checked again on the thirteenth and fifteenth day (12 and 14 days old). On the thirteenth day all young in the brood were ringed. On both the thirteenth and fifteenth day each nestling was weighed and the wing length and tarsus length were recorded. Nestlings were weighed to the nearest 0.1 g with a Pesola spring balance. Tarsus length was measured to the nearest 1 mm on the folded, stretched wing from the wrist to the end of the longest primary. Measurements on the control area broods were only taken on the fifteenth day when they were weighed and ringed. As far as possible thirteenth and

fifteenth day measurements were taken in the mid-afternoon, between 1400-1700h. Each box was checked again at the end of the breeding season to ensure that no young died in the nest after the fifteenth day.

RESULTS AND DISCUSSION

Bean Wood was chosen as the removal area. All blue tit broods in nest boxes were removed when less than 3 days old. A total of 346 young were removed from 33 nests. Of these, 275 young were added to blue tit nests in the brood supplemented area, Marley. Marley blue tit nests hatched a total of 613 young at 60 nests. Thus the population of blue tit young in Marley was increased by 45 percent. Blue tit broods in Broad Oak were not manipulated and this section served as a control for the two experimental sections.

The number of great tit young in each of the three sections was not altered. In Broad Oak there were 26 great tit pairs of which 22 fledged a total of 205 young. In Marley there were 30 pairs with 27 nests fledging 237 young. Bean Wood had 18 nests of which 15 fledged 143 young. Table 7.1 summarizes the situation in the experimental and control sections of the wood. Tables 7.2 - 7.4 give the details for each great tit nest that hatched young.

Several great tit broods that were reared to the fifteenth day have been excluded from the analyses that follow. These were all nests where one parent could not be found at the time when adults were being trapped. In

Table 7.1 Summary of removal experiment in 1979.

Section	Great Tits	Blue Tits
Bean Wood Removal Area	1.06 pairs ha^{-1} 18 nests 15 successful broods	2.18 pairs ha^{-1} 37 nests 33 broods 346 young removed
Marley Supplemented Area	0.66 pairs ha^{-1} 30 nests 27 successful broods	1.56 pairs ha^{-1} 68 nests 60 broods Young increased by 45%
Broad Oak Control Area	0.73 pairs ha^{-1} 26 nests 22 successful broods	1.26 pairs ha^{-1} 45 nests 37 broods

Table 7.2. Great tit data from Marley Wood and Marley Plantation. Blue tit brood supplemented area 1979.

BOX	FIRST EGG DATE	15th DAY	CLUTCH	BROOD (MANIP.)	FLEDGED
MP46	28	65	11	11	11
MP76	28	65	10	6	6
MP67	24	65	10	9	9
MP8	28	67	12	10	10
B80A	30	67	11	10	10
MP14	33	67	9	7(+3)	10
MP52	26	67	10	7(-3)	7
MP28	25	67	11	11	11
MP43°	32	68	8	8(+3)	pred.
MP63	29	68	10	10(-3)	7
B86*	33	69	7	6	6
B194	37	70	9	9	9
MP54	32	70	11	8	8
MP51	35	71	10	10	10
B98	34	71	10	4	4
B137	38	72	9	9(+3)	12
B60	36	72	11	7	7
B66	39	75	10	10(-3)	7
B226	42	75	10	10	10
B225	39	75	11	10(+3)	13
B54	40	76	11	8(-3)	8
B63	40	76	9	7	7
B67	45	77	7	7	7
B213	43	79	10	10	10
B27	47	80	9	7	7
B10*	45	80	10	10	10
B113	44	81	12	11	11
B106	47	81	10	10	10

° Predated, not used. * One parent missing, not used.

Table 7.3. Great tit data from Broad Oak. Blue tit control area 1979.

BOX	FIRST EGG DATE	15th DAY	CLUTCH	BROOD (MANIP.)	FLEDGED
064	31	67	9	9	9
012	31	68	11	11	11
076	31	69	12	12	12
06	31	70	11	11	11
059	34	71	10	9	9
04	26(?)	71	10	9	9
054*	37	72	10	10	10
0115	39	74	8	8	8
022*	40	74	8	8	0
030	39	75	9	7	7
042	41	76	9	9	9
065	43	76	9	9	9
086	40	76	10	10(-3)	7
039	33	76	7	7(+3)	10
073	39	77	12	12	12
050	42	77	9	8	8
037	42	77	10	9	9
057	42	77	9	8	8
020	42	78	10	8	8
094	41	78	9	8	8
085	43	80	12	12	12
075C	44	80	11	11	11
0103	44	82	10	8	8

* One parent missing, not used.

Table 7.4. Great tit data from Bean Wood. Blue tit brood removal area 1979.

BOX	FIRST EGG DATE	15th DAY	CLUTCH	BROOD (MANIP.)	FLEDGED
C160	34	69	8	8	8
C20	34	69	11	11	11
C147	34	69	8	6	6
C26*	38	73	10	9	9
C55	40	75	9	9	9
C130	38	75	8	8	8
C4	40	76	11	10	10
C136	40	76	11	11	11
C111	43	79	11	11	11
C115	42	79	14	14(-3)	11
C9	44	79	10	8	8
C62	44	79	9	8(+3)	10
C135	46	79	10	10	10
C145	45	80	10	9	9
C131	44	85	14	12	12

* One parent missing, not used.

one instance, B86, the male had been fitted with a radio transmitter and he stopped feeding the brood. In the remaining instances, B10, C26 and 054, one parent was probably taken by sparrow hawks. Thus fifteenth day weights from 14 Bean Wood, 21 Broad Oak and 25 Marley broods are used.

In both Marley and Bean Wood great tit wing, tarsus and weight measurements were made on the thirteenth and fifteenth day. However, the three earliest broods in Marley were not visited on the thirteenth day. Thus thirteenth and fifteenth day measurements were taken from 22 broods in Marley and 14 broods in Bean Wood.

Fifteenth-day weights of great tits

The primary prediction tested by the blue tit brood manipulation experiment was that great tit fledging weight (fifteenth-day weight) would increase if blue tit young were removed from an area and decrease if blue tit broods were supplemented with additional young. This is just the result obtained. Broods in Marley were lightest, Bean Wood broods were heaviest, and Broad Oak broods were intermediate in weight (Table 7.5).

The brood weights might have been biased by factors other than the experimental manipulations. For example, the habitat in one of the sections of the wood could have led to consistently higher brood weights. Table 7.6 shows that there has been no significant difference between the mean fledging weights in the three sections of the wood whereas there have been significant differences between the fledging weights in different years. Also, in no

Table 7.5. Results from removal experiment, great tit fledging weights.

Section	Mean Fledging Weight (g)	Standard Error	Sample Size
Removal Area Bean Wood	19.94	0.27	14
Supplemented Area Marley	18.75	0.18	25
Control Area Broad Oak	19.03	0.14	21

Control vs Removal	$t = 3.25$, $P < 0.01$
Control vs Supplemented	$t = 1.17$, n.s.
Removal vs Supplemented	$t = 3.72$, $P < 0.001$

Table 7.6. Means of mean brood weights in three areas of the wood over nineteen years. Sample size in brackets after means.

YEAR	BEAN	MARLEY	BROAD OAK	MEAN[a]
60	(19.03)[a]	18.62 (40)	19.34 (15)	19.00
61	18.93 (14)	18.15 (55)	18.62 (26)	18.57
62	18.37 (18)	18.11 (46)	19.06 (23)	18.51
63	19.34 (16)	18.78 (47)	19.20 (27)	19.11
64	18.61 (19)	18.36 (37)	18.89 (12)	18.62
65	19.34 (4)	19.26 (47)	18.88 (27)	19.16
66	18.66 (8)	18.14 (41)	18.11 (15)	18.30
67	19.34 (11)	18.47 (30)	18.56 (10)	18.79
68	(18.34)[a]	18.01 (18)	18.57 (12)	18.31
69	(19.19)[a]	19.80 (4)	18.49 (14)	19.16
70	(19.63)[a]	19.52 (15)	(19.66)[a]	19.60
71	18.83 (7)	19.41 (46)	19.34 (21)	19.19
72	18.50 (8)	19.33 (35)	19.44 (6)	19.09
73	19.51 (13)	18.93 (44)	19.23 (3)	19.19
74	18.81 (16)	18.45 (29)	18.85 (8)	18.70
75	18.21 (20)	19.00 (38)	18.90 (21)	18.70
76	19.31 (13)	19.13 (29)	19.14 (16)	19.19
77	18.95 (25)	18.88 (35)	18.97 (16)	18.93
78	18.56 (24)	18.71 (37)	18.61 (22)	18.63
MEAN[a]	18.91	18.79	18.94	18.88

ANOVA

FACTOR	D.F.	SS%	MS	F-RATIO	P<
Area	2	2.5	0.120	0.85	n.s.
Year	18	69.3	0.363	2.63	0.02
Residual	35[a]	45.3	0.138		
Total	51	117.1	0.217		

[a] Corrections made for missing data

year has there been a difference between the mean great tit fledging weights of Bean Wood and Marley broods as great as that resulting from the experiment. While that is encouraging it has already been shown that the mean fledging weights of great tit broods is related to several factors including section of the wood, blue tit density, number of young fledged and first egg date.

The multiple regression model for great tit fledging weight (Table 6.9) can be used to predict a mean fledging weight for each brood. The fledging weight predicted is subtracted from the observed fledging weight to obtain a residual weight which should represent an unbiased measure of the effect of the experiment. There were significant differences between the mean residuals for the three areas (ANOVA $F_{2,57}=5.78$, $P<0.02$). Great tits in the removal area were significantly heavier than in the control or supplemented area (Table 7.7, Figure 7.1). The difference between the control area and the blue tit brood supplemented area was not significant, though it is in the predicted direction.

Figure 7.2 shows how blue tit density and section of the wood affect fledging weight according to the regression model. If there had been no blue tit manipulation the residual weights should have been the same. However, the difference between the control and supplemented areas was -0.19g and between the control and removal areas it was 0.94g. The model predicts a 0.19g drop in fledging weight if the blue tit density in Marley is increased by 0.7 pairs per hectare, i.e., a 45 percent increase over the

Table 7.7. Experimental results corrected for number of young, laying date, section of the wood, and initial blue tit density. Residual is the observed minus the expected fledging weight. The statistic 'q' is for the Neuman-Kuels multiple range test.

Section	Mean Residual (g)	Standard Error	Sample Size
Removal Area Bean Wood	0.44	0.24	14
Supplemented Area Marley	-0.50	0.18	25
Control Area Broad Oak	-0.32	0.15	21

Control vs Removal	t = 2.79, P< 0.01	q = 4.33, P < 0.01
Control vs Supplemented	t = 0.78, n.s.	q = 1.24, n.s.
Removal vs Supplemented	t = 3.13, P< 0.01	q = 5.62, P< 0.001

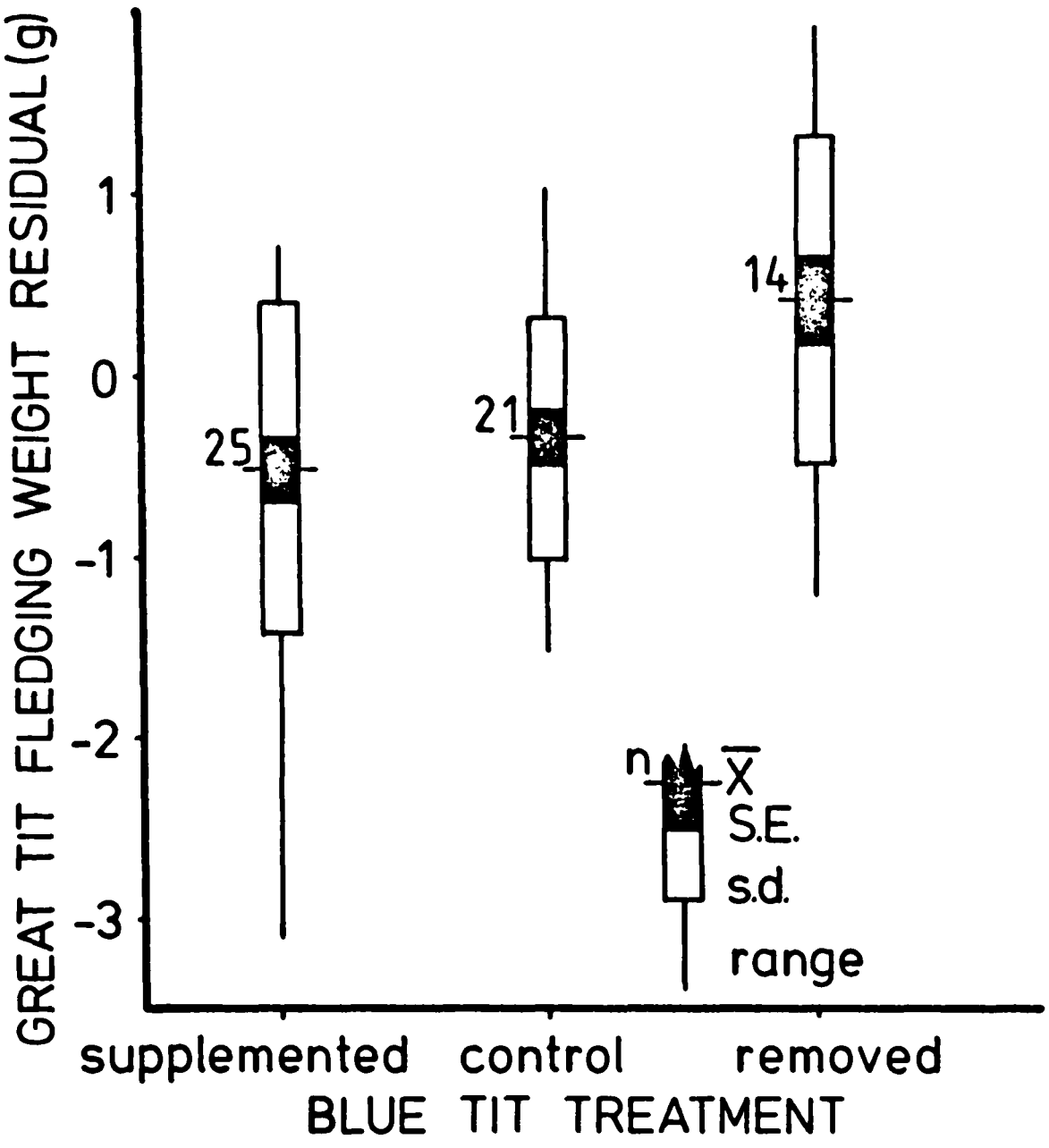


Figure 7.1 Effect of blue tit brood manipulation on the great tit fledging weight residual. The residual is the difference between the observed fledging weight for each brood and that predicted by the regression model (Table 6.9, p172). The null hypothesis is that the means for the three treatments should be the same.

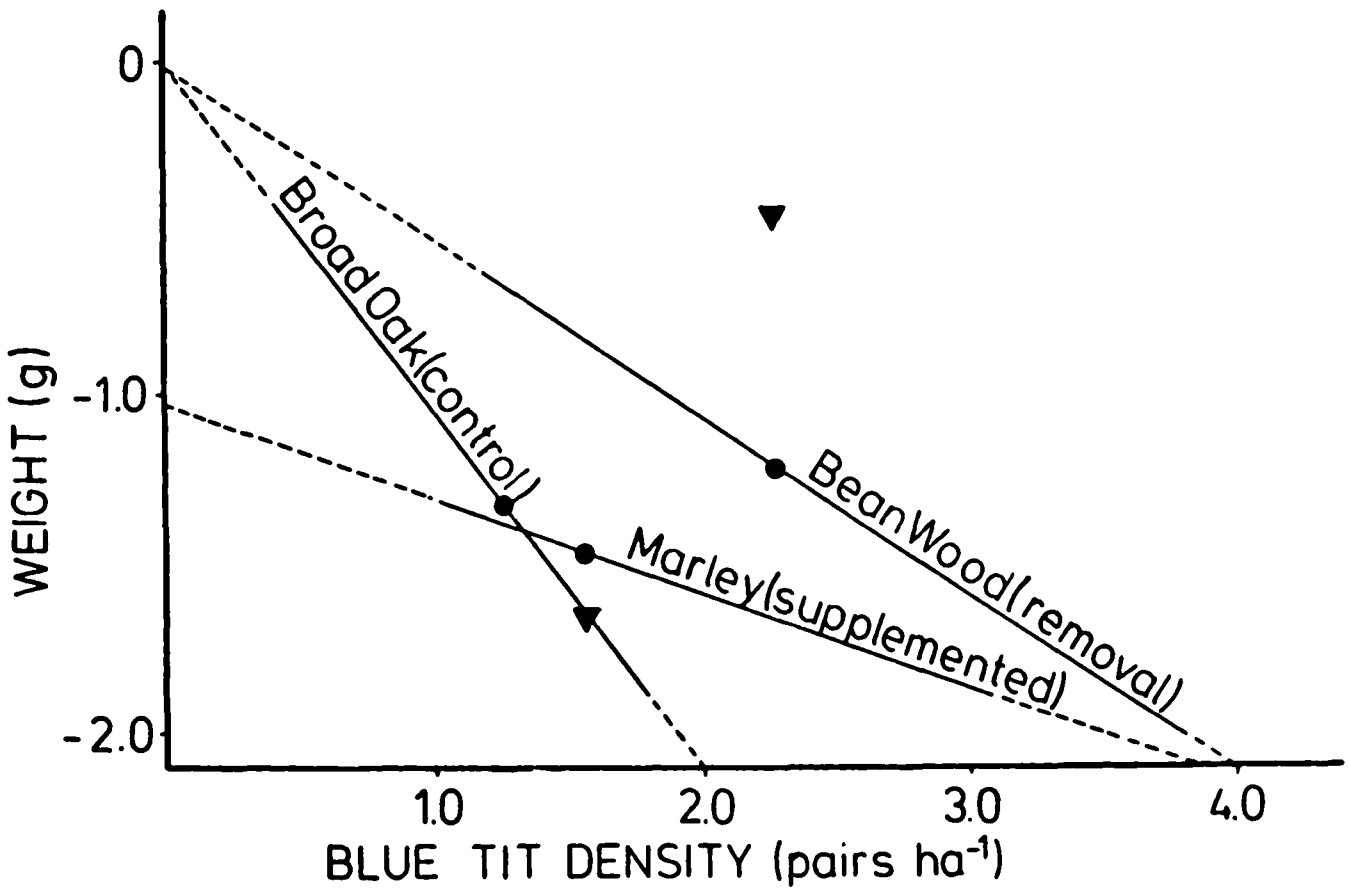


Figure 7.2 Effect of blue tit density and section of the wood on great tit fledging weight. The circles are the predicted effect on fledging weight given the 1979 breeding densities of blue tits. The triangles are the observed deviations from the predicted weights relative to the control area after correcting for first egg date and number of young fledged. The regression lines are based on Table 6.9 (p172).

1.56 pairs per hectare breeding in 1979. Although the breeding density of blue tit pairs was not changed, the number of blue tit young in Marley was increased by exactly 45 percent. This exact fit to the model is presumably fortuitous but it does show that the effects of the experiment are consistent with the prediction from the model.

The same calculation may be made for Bean Wood, the removal area. There the model predicts that the removal of all blue tits would result in a residual 1.12g greater than for the control area. In fact the difference was only 0.94g. There are several reasons for the shortfall of 0.18g. Firstly, the 0.18g discrepancy is well within the 95 percent confidence interval of the difference between the two means (0.94 ± 0.56g). Second, the prediction is an extrapolation beyond the limits of data available for the regression. It may be that at low densities of blue tits the effect on great tit fledging weights becomes non-linear. Third, the adult blue tits remained in Bean Wood and caused some depletion of the insect food.

The results from the fifteenth day weights of great tits in the three sections were consistent with the predictions from the regression model. The ability of great tits to rear young, and ultimately their reproductive success, is decreased at higher densities of blue tits.

Weight change and weight variance in great tit broods

A graph of nestling weight against time shows that the typical pattern has several important properties (Figures 7.3 and 7.4). Weight increases monotonically with time from hatching to about the sixteenth day. The curve is sigmoid. The absolute growth rate is greatest during the middle of the nestling period, around the fourth to the tenth day. Also, the variance in weight is greatest toward the end of the rapid growth period, about days 10 to 12. The variance or standard deviation increases up to this time and then decreases up to the time of fledging. This trend is even more marked if a relative measure such as the coefficient of variability is used ($V = 100s/\bar{x}$, where s is the standard deviation and $\bar{x}$ the mean).

Under favourable conditions the growth rate of nestlings is much lower between the 13th and 15th days than in the preceeding 7 to 9 days. If for some reason the growth of a brood has been retarded then their period of rapid growth should extend into the time between the 13th and 15th days. Thus broods in which growth has been retarded should show a greater weight gain from the 13th to the 15th day than broods which developed more rapidly.

Following the above argument the 13th to 15th day weight gains of the Marley broods should have been greater than for the Bean Wood broods. This is what happened (Tables 7.8 and 7.9, Figure 7.5). Marley broods gained an average of 0.85g while Bean Wood broods gained only 0.47g. Thus to some extent the Marley broods made up for

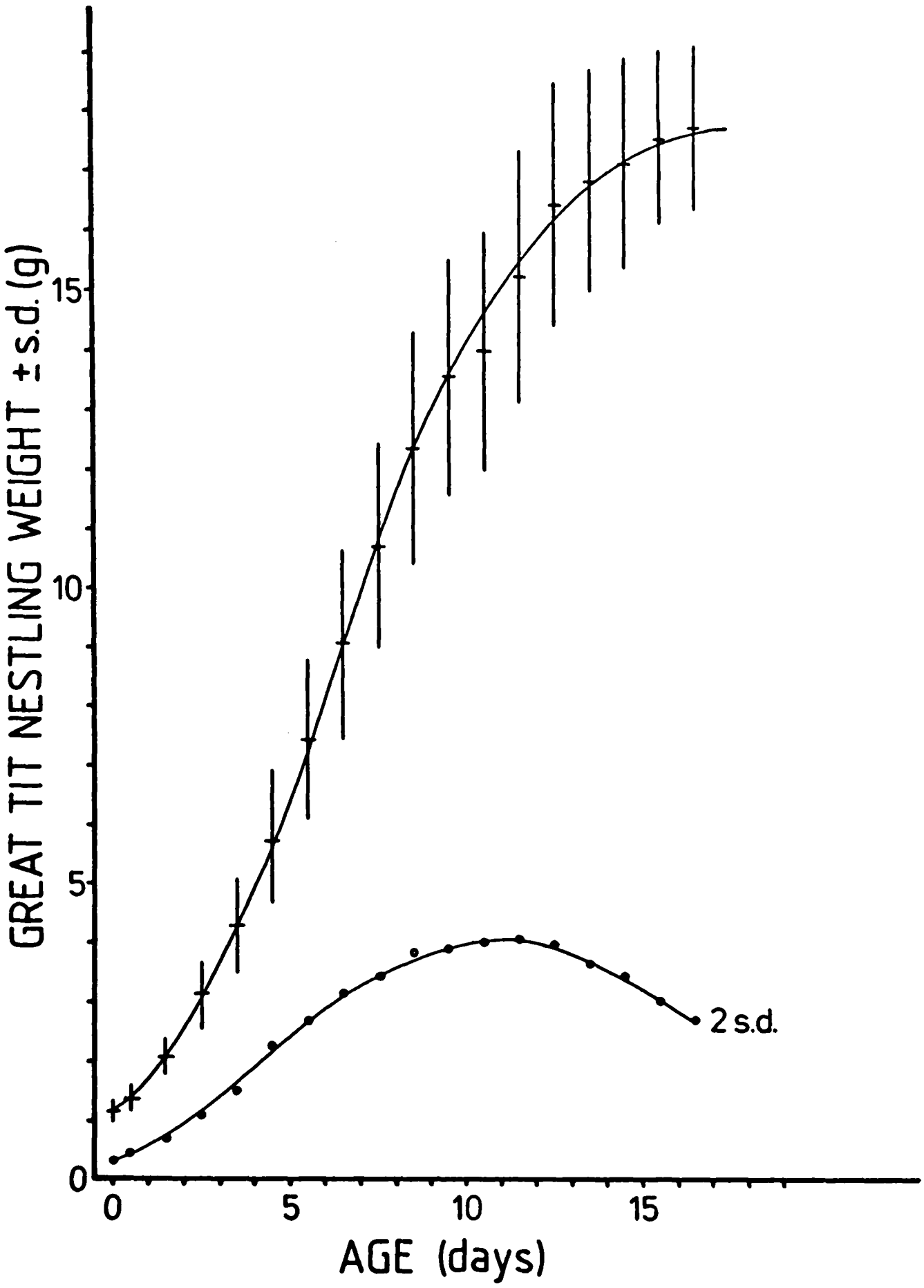


Figure 7.3 Growth curve for great tit nestlings. The standard deviation is shown by the vertical bars and is graphed separately below the growth curve. Data are from Gibb (1953) for 1950.

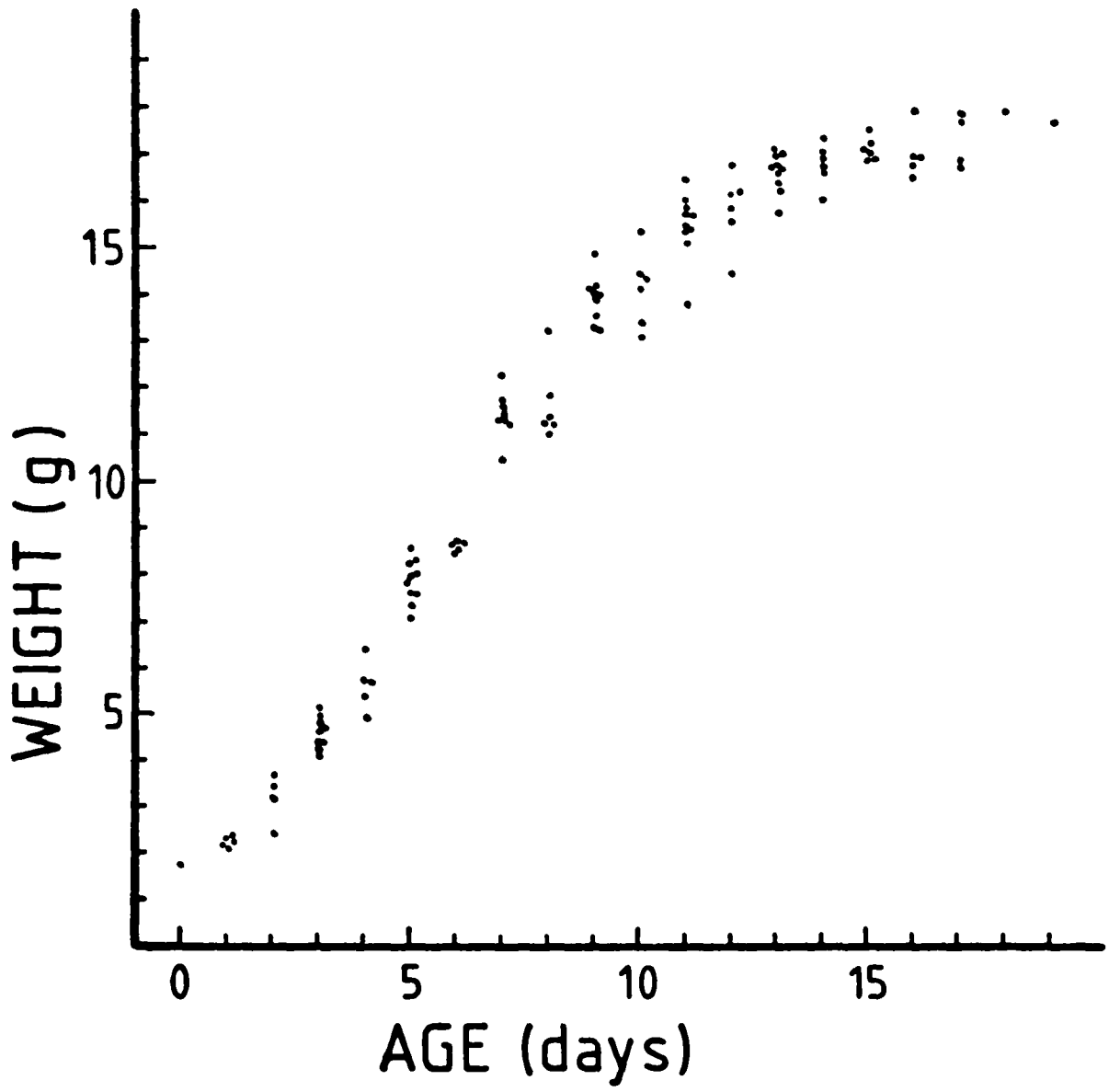


Figure 7.4 Growth curve for great tit nestlings (after van Balen 1973).

Table 7.8. Thirteenth and fifteenth day mean brood weights in Marley and Bean Wood in 1979. 'Change' is the fifteenth minus thirteenth day weights.

MARLEY				BEAN WOOD			
Box	13th	15th	Change	Box	13th	15th	Change
MP46		(18.93)		C160	19.89	20.66	0.77
MP76		(16.32)		C20	19.15	19.76	0.61
MP67		(17.93)		C147	19.20	19.97	0.77
MP8	16.85	17.60	0.75	C55	19.88	20.28	0.40
B80A	17.68	18.70	1.02	C130	20.64	21.28	0.64
MP14	16.81	17.42	0.61	C4	19.61	19.95	0.34
MP52	18.50	18.67	0.17	C136	18.29	18.85	0.56
MP28	18.12	18.78	0.66	C111	20.05	20.43	0.38
MP63	17.43	19.59	2.16	C115	17.80	18.65	0.85
B194	18.34	19.20	0.86	C9	21.08	21.35	0.27
MP54	17.68	18.56	0.88	C62	19.60	19.84	0.24
MP51	16.73	18.12	1.39	C135	18.58	19.47	0.89
B98	19.08	19.88	0.80	C145	20.79	20.86	0.07
B137	18.73	19.49	0.76	C131	18.03	17.80	-0.23
B60	18.74	19.20	0.46				
B66	18.16	19.67	1.51	$\bar{x}$	19.47	19.94	0.469
B226	17.62	18.81	1.19	s	1.02	1.01	0.320
B225	18.18	19.04	0.86	SE	0.274	0.269	0.085
B54	18.44	19.05	0.61				
B63	20.14	20.27	0.13				
B67	17.63	18.83	1.20				
B213	16.19	17.56	1.63				
B27	19.07	19.33	0.26				
B113	18.96	19.95	0.99				
B106	18.82	18.77	-0.05				
$\bar{x}$	18.08	18.93	0.857				
s	0.930	0.766	0.526				
SE	0.200	0.163	0.112				

Table 7.9. Summary of great tit nestling weights on thirteenth and fifteenth days and weight change from the thirteenth to fifteenth day (g ± S.E.).

	13^{th}	15^{th}	Change	n(d.f.)
MARLEY	18.08 ± 0.20	18.93 ± 0.16	0.85 ± 0.11	22
BEAN WOOD	19.47 ± 0.27	19.94 ± 0.27	0.47 ± 0.10	14
DIFFERENCE	-1.39	-1.01	0.39	
t-test	4.19	3.41	2.48	(34)
One-tailed P	0.0005	0.001	0.01	

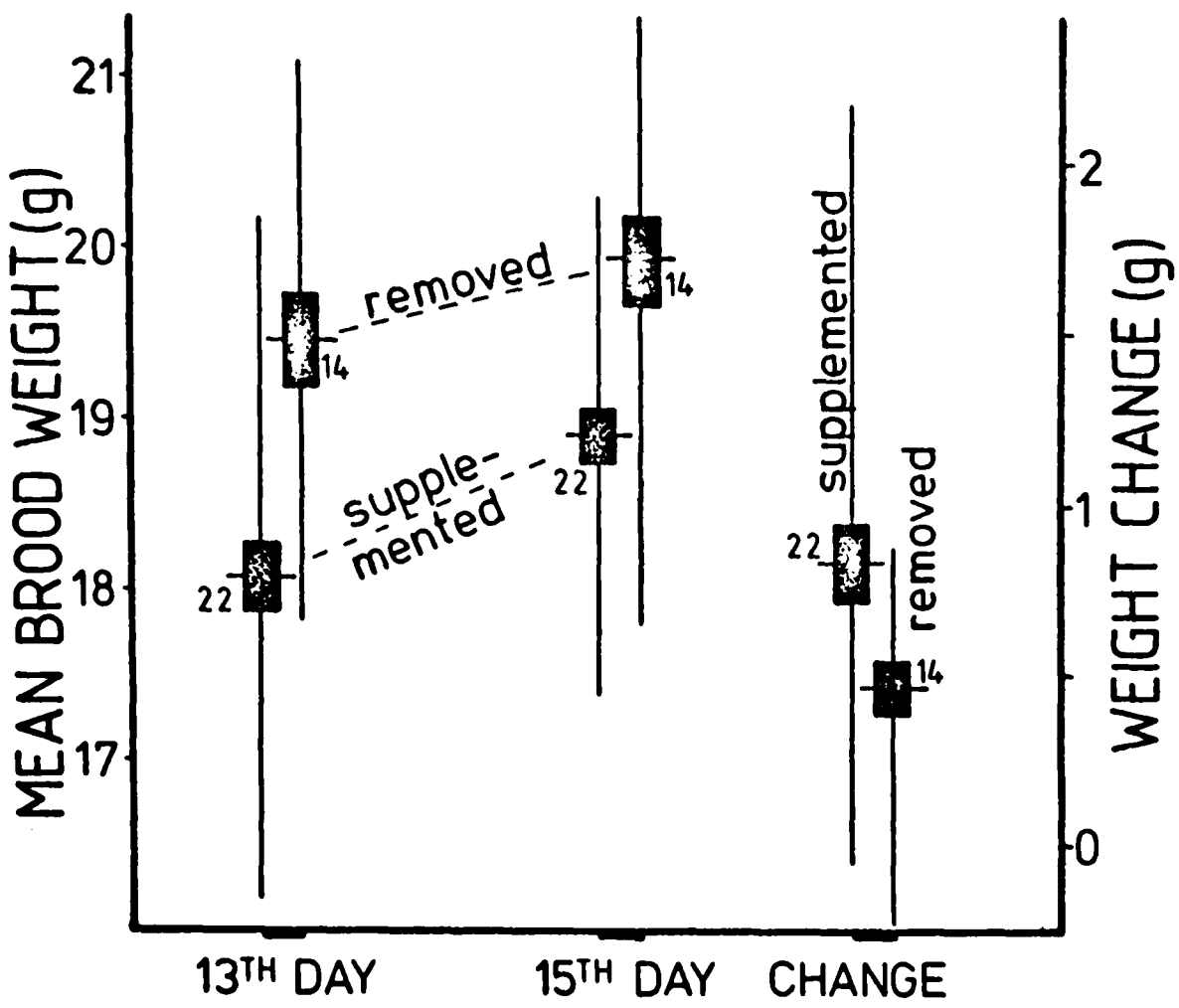


Figure 7.5 Effect of blue tit treatment on the weights of great tit nestlings. The thin line is the range and the heavy, black bar is the standard error of the mean.

their slower growth rate by extending the period of growth.

This result suggests that the 13th day might actually be a better time to detect differences between nestling weights than the traditional 15th day used in Wytham. Both the within brood and between brood variance is greater on the 13th day than the 15th day (Table 7.10). However, the t-value for the difference between Marley and Bean Wood (ratio of the difference to the standard error of the difference) was greater on the 13th day than on the 15th day (Table 7.9). This indicates that the greater difference in mean weights on the 13th day more than offsets the greater standard error of the difference and thus may be better suited to detect differences in weight development than 15th day weights.

The trend toward decreasing variance in weight from about the 10th day is a final check that the great tit broods were more retarded in weight development at higher densities of blue tit young. Those broods that are more advanced on the 15th day should have a lower variance in weight.

The formation of a proper null hypothesis is important. One test is whether the variances of the means of all brood means in the areas are different in two or more of the sections of the wood. For this Bartlett's homogeneity of variances test would be applicable. In fact there is no significant difference amongst the three areas, Bean Wood, Marley and Broad Oak ($0.25 < P(B_c \geq 1.43) < 0.50$). This result legitimizes the use of analysis of variance or

Table 7.10. Within and between brood standard deviations of weight on thirteenth and fifteenth day. Between brood standard deviation is the standard deviation of the mean brood weight in each category. Within brood standard deviation is the mean of the standard deviations of all brood mean weights in each category.

		WITHIN BROOD STANDARD DEVIATION	BETWEEN BROOD STANDARD DEVIATION
MARLEY	13^{th}DAY	0.99	0.93
	15^{th}DAY	0.87	0.77
BEAN WOOD	13^{th}DAY	0.87	1.02
	15^{th}DAY	0.77	1.01

t-tests to test for differences in the mean weight amongst the three areas but there are two reasons why it is not a satisfactory test for a significant experimental result. First, between brood variance may be more of a measure of habitat heterogeneity than a measure of the experimental effect. Second, the test compares the variance of three groups with significantly different means. Instead, a test is needed to determine whether variability within broods in each area is different. Lewontin (1966) has shown that 'the variance (or standard deviation) of the logarithms of measurements gives a measure of intrinsic variability which is invariate under multiplicative change'. Thus no matter what the mean weight of a brood the standard deviation of the log weight should be the same if all broods have the same amount of variability. The null hypothesis is that the standard deviations of the mean log weights of the great tit broods under the three treatments do not increase with increased density of blue tits.

The standard deviations of log weights in the three areas are compared in Table 7.11 and Figure 7.6. Although the standard deviations are approximately normally distributed the non-parametric Kendall's ranked categories test was used to test the null hypothesis. There is a significant positive correlation between ranked treatments (manipulation of blue tit nestling density) and ranked standard deviations (Kendall's $\tau = 0.21$, $Z = 2.33$, $P < 0.01$, one-tailed).

So far I have shown that the fledging weights of great tits were significantly affected by the manipulation of

Table 7.11. Standard deviations of $\log_e$ fledging weights of great tit broods in blue tit supplemented area (Marley), control area (Broad Oak), and removal area (Bean Wood). Standard deviations have been multiplied by 100.

MARLEY		BROAD OAK		BEAN WOOD	
Box	s_{ln}	Box	s_{ln}	Box	s_{ln}
MP46	4.84	064	4.20	C60	3.26
MP76	8.51	012	6.14	C20	2.75
MP67	6.12	076	4.94	C147	1.96
MP8	4.01	06	3.07	C55	3.69
B80A	4.39	059	3.33	C130	1.76
MP14	7.21	04	3.48	C4	3.41
MP52	2.28	0115	6.63	C136	7.11
MP28	4.46	030	2.42	C111	2.91
MP63	3.06	042	5.53	C115	3.02
B194	3.70	065	5.82	C9	4.06
MP54	4.47	086	3.70	C62	4.51
MP51	2.58	039	4.80	C135	4.04
B98	4.18	073	2.74	C145	3.42
B137	6.63	050	5.83	C131	5.31
B60	3.55	037	4.48		
B66	3.19	057	6.37		
B226	7.30	020	3.46		
B225	7.60	094	2.93		
B54	4.57	085	4.05		
B63	4.28	075C	4.14		
B67	3.86	0103	2.13		
B213	4.44				
B27	7.09				
B113	5.81				
B106	3.97				
$\bar{s}$	4.88		4.31		3.66
$s_{\bar{s}}$	1.68		1.38		1.37
$SE_{\bar{s}}$	0.337		0.301		0.365
n	25		21		14

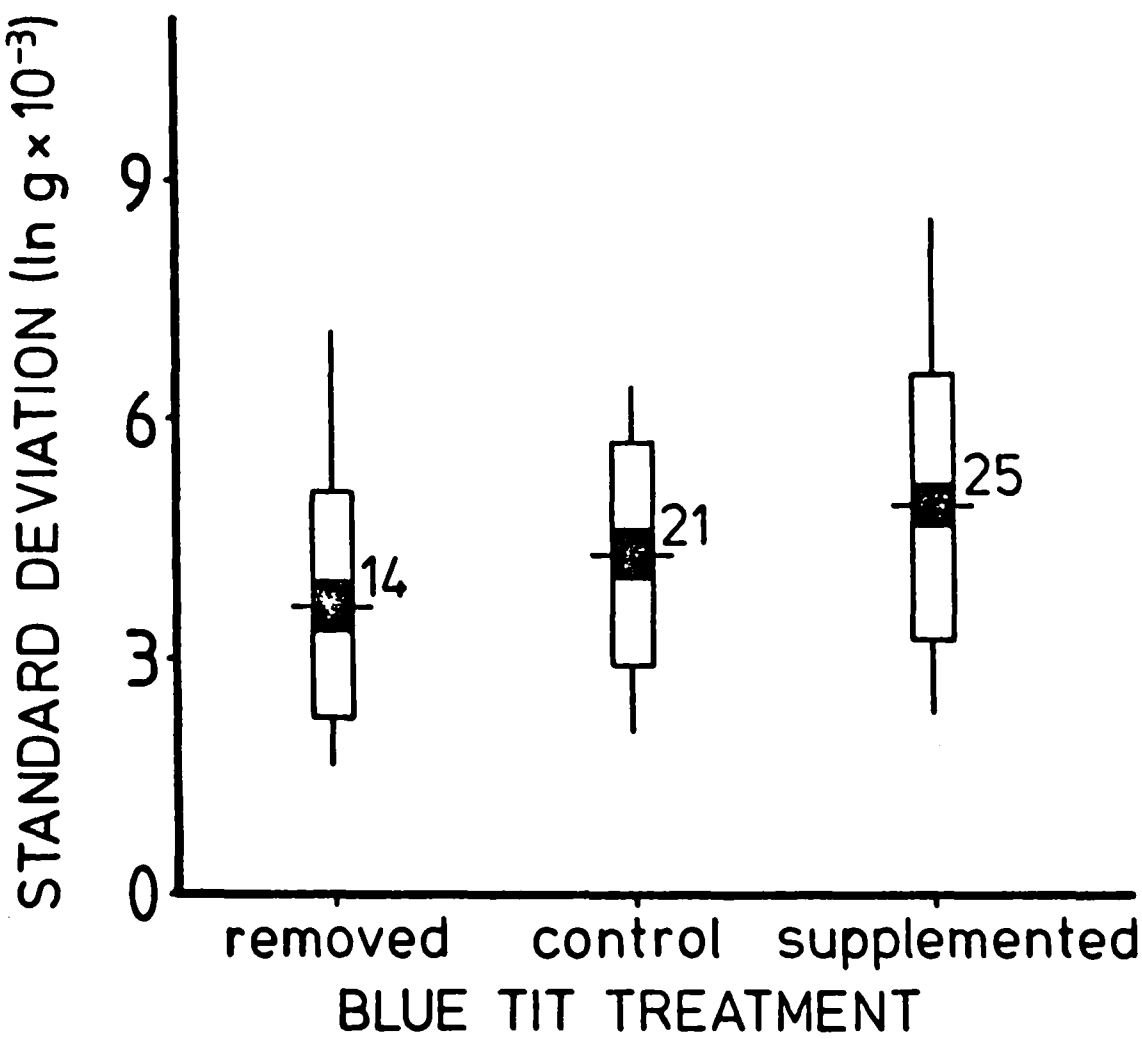


Figure 7.6 Effect of blue tit nestling manipulations on the standard deviation of great tit nestling weights within broods. The thin vertical lines are the ranges, the open bars are the standard deviations, and the closed bars are the standard errors of the mean.

blue tit young and that the magnitude of the effect was consistent with the regression model based on historical data. Also, the period of rapid growth lasted longer in great tit broods in the area of greatest competition with blue tits. Finally, the within brood variance in log weight increased with the density of blue tit young. These three significant results were a priori predictions based on fledging weight data for the three areas and growth data for the great tit.

Wing length and tarsus measurements

Much less is known about wing and tarsus growth in great tits. Garnett (1976) discusses aspects of these measurements for 15th-day nestlings and their relationship to future development and survival. He concluded that nestling weight was the best measure of actual body size but that tarsus length was a better indicator of eventual adult size. Wing length varied significantly with hatching order and was thought to be a good indicator of nestling development but of no use in predicting adult size. Tarsus length was found to have a high degree of heritability (about 75 percent), the remaining variation due mostly to date of hatching and between year effects. Both fledging weight and tarsus length were correlated with survival in a limited sample, although wing length was not.

O'Connor (1973) studied growth in the closely related blue tit. He showed that weight peaked on the 15th day, the tarsus was fully grown on the 11th day and that after the 11th day all growth in winglength was feather growth which was continuous until after fledging. The growth

curve for total winglength was only slightly sigmoid. The coefficient of winglength variation decreased linearly from about day 5 to day 15.

Using the above results it is possible to make some predictions about length and growth of wings and tarsi in the two experimental areas. Because maximum tarsus length should be achieved early in the nestling period there should be no significant difference in growth from the 13th to 15th days. Also, because of the high heritability of tarsus length there should be no significant difference in tarsus length between the two areas unless the environmental component is very strong. The wing lengths of the removal area birds should, if anything, be longer than for the blue tit supplemented area because the nestlings should develop faster if more food is available. Also, the 13th to 15th day wing length growth of great tit nestlings may be slower in the removal area if they have already passed the time of most rapid growth. Finally, the within brood variance in winglength may be lower for physically more advanced broods, especially on the 15th day, as shown by O'Connor (1973) for blue tits and in the previous section for great tit nestling weights.

As expected, there were no significant differences in tarsus length or growth rate in the two areas (Tables 7.12 and 7.13, Figure 7.7). There was also no significant difference in the within nest variance of log tarsus length between Bean Wood and Marley on either the 13th or 15th days. While there were no significant differences between broods under the two treatments it is noteworthy

Table 7.12. Thirteenth and fifteenth day mean tarsus lengths of broods in Bean Wood and Marley in 1979. 'Change' is the fifteenth minus thirteenth day lengths.

MARLEY				BEAN WOOD			
Box	13th	15th	Change	Box	13th	15th	Change
MP46		(20.58)		C160	20.39	20.71	0.32
MP76		(19.97)		C20	20.57	20.83	0.26
MP67		(20.50)		C147	20.45	20.68	0.23
MP8	19.50	19.91	0.41	C55	20.34	20.52	0.18
B80A	19.98	20.42	0.44	C130	20.36	20.45	0.09
MP14	19.95	20.36	0.41	C4	19.72	20.11	0.39
MP52	20.41	20.56	0.15	C136	19.59	19.99	0.40
MP28	19.88	19.99	0.11	C111	19.88	20.12	0.24
MP63	20.14	20.71	0.57	C115	19.65	20.05	0.40
B194	20.23	20.34	0.11	C9	20.20	20.63	0.43
MP54	20.21	20.41	0.20	C62	20.44	20.66	0.22
MP51	19.41	19.89	0.48	C135	19.44	20.34	0.90
B98	20.08	20.23	0.15	C145	20.39	20.54	0.15
B137	20.31	20.56	0.25	C131	19.77	19.83	0.06
B60	19.50	20.06	0.56				
B66	20.27	20.54	0.27	$\bar{x}$	20.09	20.39	0.31
B226	19.88	20.38	0.50	s	0.39	0.32	0.21
B225	20.02	20.00	-0.02	SE	0.104	0.084	0.055
B54	20.01	20.23	0.22				
B63	19.91	20.27	0.36				
B67	18.83	19.50	0.67				
B213	19.10	19.76	0.66				
B27	20.41	20.74	0.33				
B113	20.23	20.28	0.05				
B106	20.06	20.25	0.19				
$\bar{x}$	19.93	20.25	0.32				
s	0.42	0.31	0.20				
SE	0.089	0.066	0.043				

Table 7.13. Summary of great tit nestling wing and tarsus lengths on thirteenth and fifteenth days and growth from thirteenth to fifteenth day (mm ± S.E.)

WING LENGTH

	13th	15th	Change	n(d.f.)
Marley	43.50 ± .456	50.08 ± .394	6.58 ± .156	22
Bean Wood	46.44 ± .75	52.38 ± .59	5.94 ± .35	14
Difference	-3.04	-2.35	0.64	
t-test	3.51	3.36	1.86	(34)
One-tailed P	0.001	0.001	0.05	

TARSUS LENGTH

	13th	15th	Change	n(d.f.)
Marley	19.93 ± .089	20.25 ± .066	0.32 ± .043	22
Bean Wood	20.09 ± .104	20.39 ± .084	0.31 ± .055	14
Difference	-0.16	-0.15	0.01	
t-test	1.16	1.37	0.143	(34)
One-tailed P	0.15	0.10	n.s.	

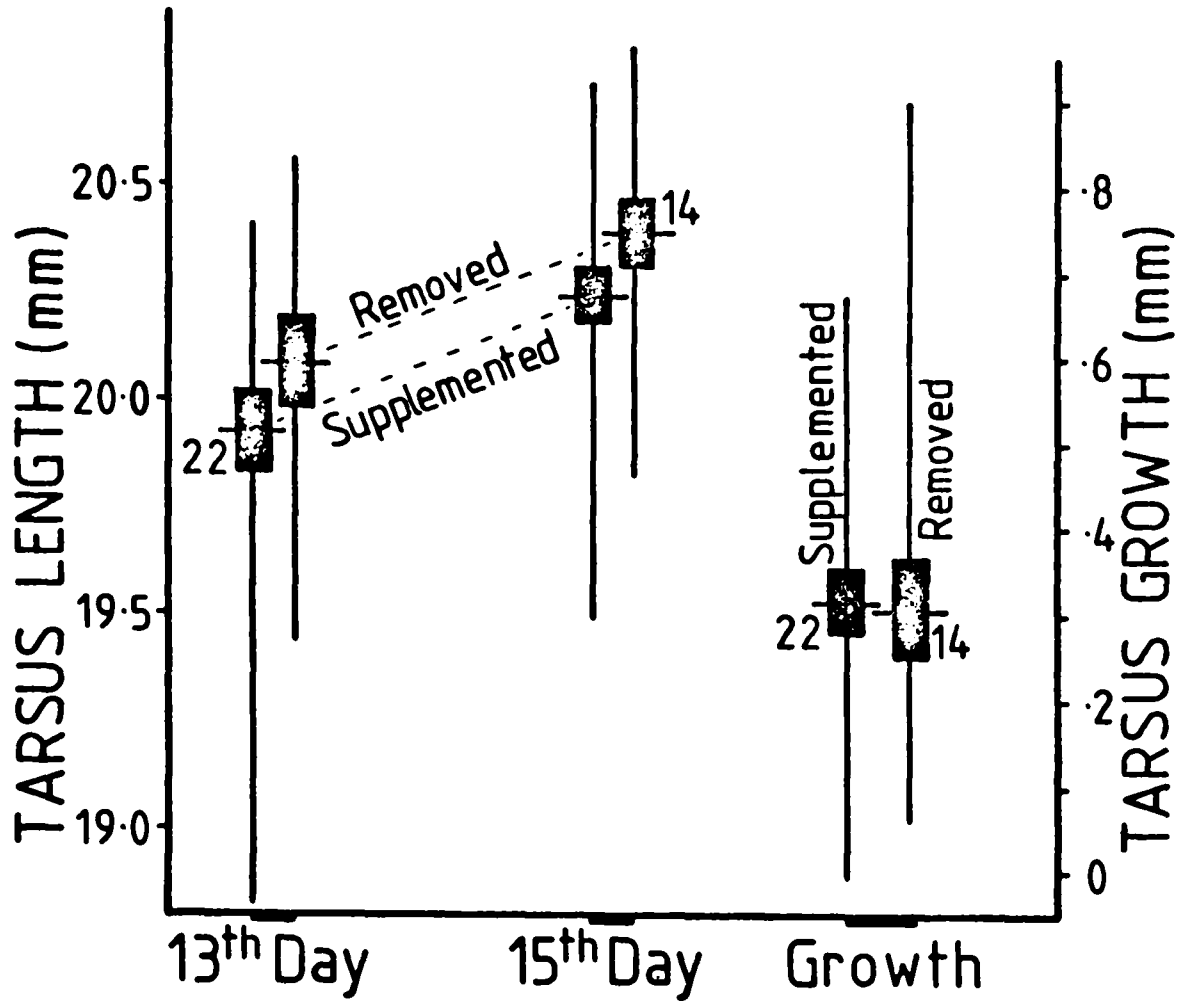


Figure 7.7 Effect of blue tit treatment on the tarsus lengths of great tits.

that in apparent contrast to blue tits there was very significant tarsus growth between the 13th and 15th days in the two sections of the wood (paired t-test on brood means pooled from the two areas, d=0.32mm, SE=0.33mm, t=9.47, n=36, $P < 0.0005$).

In contrast to tarsus length, great tit wing length was significantly different under the two blue tit treatments on both the 13th and 15th days, being longer in the removal area than the supplemented area. Also, the wing length growth rate was slower in the removal area (Tables 7.13 and 7.14, Figure 7.8). The standard deviations of log wing length within broods of removal area nestlings were not significantly different from supplemented area nestlings on the 15th day (Mann-Whitney test, Z=0.68, $P < 0.25$, one-tailed). However, the mean standard deviation was lower in the removal area ($\bar{s}_{ln} = 0.036$) than in the supplemented area ($\bar{s}_{ln} = 0.046$). There was a tendency toward a negatively skewed distribution of winglengths within nests as occurred to a lesser extent with weight and tarsus length. This was particularly pronounced in broods containing one late hatching nestling which contributed to a high variance. I attempted several methods of correcting for this but the variance in the two areas was still not significantly different.

Table 7.14. Thirteenth and fifteenth day mean wing lengths of broods in Marley and Bean Wood in 1979. 'Change' is the fifteenth minus thirteenth day lengths.

MARLEY				BEAN WOOD			
Box	13th	15th	Change	Box	13th	15th	Change
MP46		(49.95)		C160	49.88	52.00	2.12
MP76		(41.17)		C20	43.09	50.91	7.82
MP67		(48.67)		C147	44.17	51.17	7.00
MP8	41.20	48.00	6.80	C55	48.63	54.67	6.04
B80A	41.40	47.90	6.50	C130	47.75	53.88	6.13
MP14	41.00	47.70	6.70	C4	43.80	49.60	5.80
MP52	42.71	48.86	6.15	C136	43.18	48.91	5.73
MP28	44.27	49.64	5.37	C111	50.00	54.91	4.91
MP63	41.14	49.86	8.72	C115	44.45	50.73	6.28
B194	45.22	51.56	6.34	C9	46.75	52.63	5.88
MP54	42.25	48.38	6.13	C62	48.50	54.40	5.90
MP51	41.50	48.20	6.70	C135	42.60	50.00	7.40
B98	45.50	51.50	6.00	C145	50.00	55.78	5.78
B137	44.50	50.75	6.25	C131	47.42	53.75	6.33
B60	42.86	50.14	7.28				
B66	45.14	52.29	7.15	$\bar{x}$	46.44	52.38	5.94
B226	41.20	48.70	7.50	s	2.80	2.21	1.33
B225	45.31	51.46	6.15	S.E.	0.75	0.59	0.35
B54	44.00	50.13	6.13				
B63	45.00	50.71	5.71				
B67	42.57	49.29	6.72				
B213	40.30	47.78	7.48				
B27	46.29	52.71	6.42				
B113	48.36	54.18	5.82				
B106	45.40	52.30	6.90				
$\bar{x}$	43.50	50.08	6.58				
s	2.14	1.85	0.734				
S.E.	0.456	0.394	0.156				

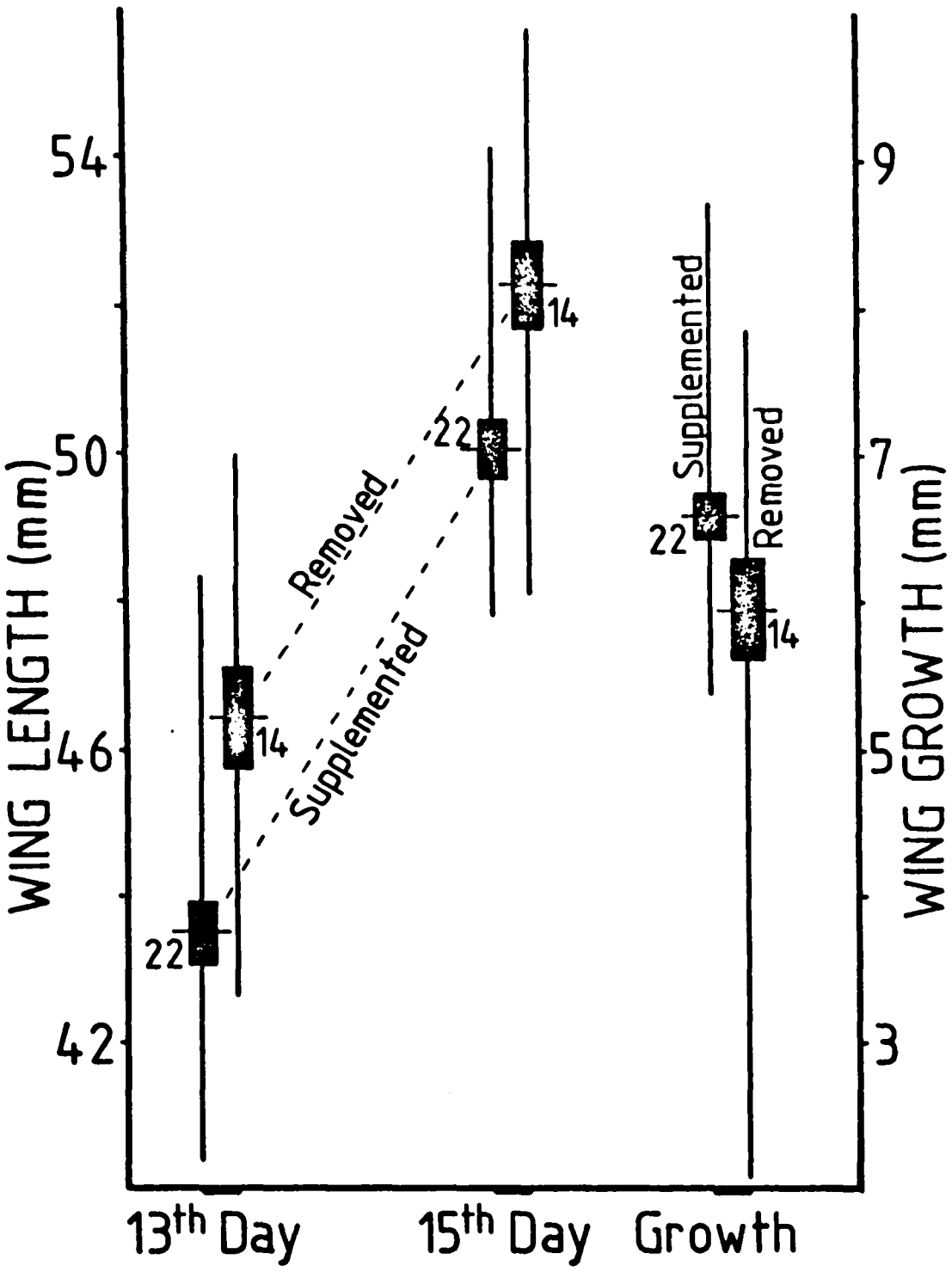


Figure 7.8 Effect of blue tit treatment on the wing lengths of great tit nestlings.

Effect of experiment on female condition

If scramble competition was relaxed by the removal of blue tit young the great tit adults should have had an easier time feeding their young. Even if they fed their young more food the adults may not have been as hard pressed as they would have been in the presence of more blue tits. If this was true the adult great tits with less competition from blue tits should have been in better condition at the end of the nesting period than great tits in the area with more blue tits. Thus the prediction is that the weights of adult female great tits in Bean Wood should have been greater than in Marley. This is what happened. Nine females in Bean Wood weighed an average of 19.20 $\pm$ 0.33 g ($\pm$S.E.) while the average weight of sixteen Marley females was 18.48 $\pm$ 0.20 g ($t=2.00$, $P < 0.05$, one-tailed).

The difference between the two areas is significant but several assumptions must be made if the difference is to be attributed to the experiment. First, the effect of great tit and blue tit density on great tit female weight should have been the same in the two areas. Second, the slight differences in breeding dates and capture dates should not bias the results. Unfortunately, female weights were first recorded in 1978 so that a regression model for predicting female weights can not be developed. The 1978 female weights for Bean Wood and Marley were not significantly different but the great tit density in Bean Wood was much higher in 1978 than in 1979 and the blue tit densities in Bean Wood and Marley were manipulated. It

is likely that the 1979 blue tit manipulation caused great tit females in the removal area to enter the post-fledging period in better condition but more work needs to be done on adult survival in relation to competition.

CONCLUSIONS

The blue tit brood manipulation experiment confirms that great tit breeding success is depressed at high densities of blue tits. The best confirmation came from great tit fledging weight which is known to be correlated with nestling survival and which could be compared with previous years' data. Not only were great tit broods in the blue tit removal area significantly heavier but the broods in both the supplemented and removal section differed from the control area by an amount consistent with the predictions of the regression model for fledging weight discussed in Chapter Six.

Thus, the within year breeding success of great tits was significantly improved by relaxing interspecific scramble competition during the nestling period. There are several reasons for suspecting that the measured differences under rather than overestimate the long term effects of competition. First, greater densities of blue tits may cause great tits to lay later in the season (Chapter Five) and this may decrease the clutch size of the great tits. Second, competition during the egg laying and incubation period may depress breeding success though historic data suggest that the effect of blue tit density at this time is of relatively minor importance. Third, mortality in the immediate post-fledging period is

thought to be high, in large part because of competition for food (Perrins 1965). If there are fewer congeners competing for food, survival should be higher. Fourth, the reduced competition may increase the lifetime fitness (Charnov and Krebs 1974) of the adults by lowering their stress during the breeding season and hastening their recovery during the post-fledging period.

Lower predation is a fifth possible reason for an underestimate of the improvement of great tit breeding success at lower densities of blue tit young. This experiment has shown that great tit nestlings reared at lower densities of blue tit nestlings were physically better developed for their age. They were larger and growth from the 13th to 15th day was slower than for great tit nestlings at higher densities of blue tit young. There was a lower within brood variance of chick weight and possibly wing length, probably as a result of the greater food supply and slower growth rate between the 13th and 15th days. The faster development probably resulted in fewer and less audible begging calls and earlier fledging. Both of these results would tend to reduce nest predation. In addition, the probability that a nest will be predated has been positively correlated with the combined density of blue and great tit pairs (Dunn 1977). The regression of survival against fledging weight would account for any effect of earlier fledging due to heavier weight. However, predation occuring prior to the 15th day would not be included and this should tend to be greater at higher densities of blue tits.

There is a possible exception to the predation argument. The sparrow hawk population has been increasing in Wytham and this species is now thought to account for a substantial percentage of the mortality of fledging tits (Geer 1979). If blue tits act as a buffer species for great tits then there are conditions under which the presence of blue tits would lower the predation of great tits though not necessarily to the extent that the buffering offsets the blue tits' other negative effects on the great tits.

CHAPTER 8

Summary

1. Nest boxes were a limiting resource for both blue and great tits. As the density of nest boxes increased, the density of breeding blue and great tits increased.
2. In sections of low nest-box density blue and great tit numbers were negatively correlated but in sections of high nest-box density the breeding numbers of the two species were positively correlated.
3. Where nest boxes were a limiting resource great tit numbers were less affected by competition than blue tit numbers and it seemed that great tits must be dominant in contests for boxes. The spatial and temporal variance of log blue tit numbers was negatively related to mean blue tit breeding densities and positively related to mean great tit breeding densities. The variance of log great tit breeding density was not related to mean breeding densities.
4. In Marley Wood, where nest boxes were at a high density, boxes were not used at random. In years of high breeding density great tits got the more favoured boxes.
5. Blue and great tits did not maintain interspecific territories or space themselves out, unless perhaps at distances of less than 20 meters. Thus interspecific interference competition during the breeding season probably did not extend far beyond the actual nest sites.
6. In sections of the wood where nest boxes were not a limiting resource the numbers of blue and great tits

fluctuated in parallel, apparently in response to environmental, density-independent factors.

7. The changes in great tit numbers from one year to the next were negatively related to the density of breeding blue tits in the previous year and positively correlated with the beech crop. Changes in blue tit density were not related to the densities of great tits but to beech crops and spring or winter temperatures. The effect of blue tit density on great tits was only applicable to population data from areas with high breeding densities and a surplus of nest sites.
8. Overlap in feeding sites of blue and great tits was greatest during the spring and summer and interspecific interference competition was least during this time. During the nestling period there was a high overlap in the nestling diets of the two species and the niche widths of the two species were similar.
9. Food was abundant during the nestling period but adults were still pressed to successfully rear a large clutch. Food for nestlings was probably a limiting resource that was significantly depleted through scramble competition.
10. Great tit first egg dates were affected by spring temperatures and great and blue tit breeding densities. Blue tit first egg dates were not affected by breeding densities. Great tits may have been more sensitive to competition during the pre-laying period than blue tits.
11. Great tit dispersal distanccs were negatively related to blue tit density for male great tits and positively

related to blue tit density for female great tits.

12. Blue and great tit clutch sizes were density dependent but inter- and intraspecific relationships were not clear. Where significant effects of interspecific density could be detected, both blue and great tit clutch sizes were negatively related to interspecific density.
13. The weights of great tits at fledging were negatively related to blue tit density. Great tit fledging weights have been positively correlated with the probability that a fledgling survives to breed.
14. As part of an experiment, blue tit young were removed at hatching from nest boxes in one section of Wytham Woods and added to broods in a second section. A third section served as a control. In the section from which blue tits were removed, the fledging weights of great tits were significantly heavier than in either the control or blue tit supplemented section. The results fit closely a regression model based on data from previous years. There were data to suggest that female condition was improved by the competitive release from blue tits.
15. Other measures of nestling growth in the two experimental sections (blue tit broods removed or supplemented) showed that great tit broods developed faster with less competition from blue tits.
16. Blue and great tits were both in competition for very similar resources during the breeding season. Generally, blue tits appeared to be the better scramble competitors (primarily for food) while great tits were the better interference competitors (primarily for breeding sites

but perhaps for food as well). These different competitive strategies may extend into the winter.

17. Competitive strategies may themselves form niche dimensions. A dynamic equilibrium for the populations of the two species may occur, in part, through temporal and spatial heterogeneity of the environment.

REFERENCES

Abbott, I., L.K. Abbott and P.R. Grant. 1977. Comparative ecology of Galapagos ground finches (Geospiza Gould): Evaluation of the importance of floristic diversity and interspecific competition. Ecological Monographs 47: 151-184.

Adams, J. 1980. The role of competition in a freshwater flat worm, Bdellocephala punctata (Turbellaria, tricladida). J. Anim. Ecol. 49:565-579.

Armstrong, R.A. and R. McGehee. 1980. Competitive exclusion. Amer. Nat. 115:151-170.

Ayala, F.J., M.E. Gilpin and J.G. Ehrenfeld. 1973. Competiti between species: theoretical models and experimental tests. Theor. Pop. Biol. 4:331-356.

van Balen, J.H. 1973. A comparative study of the breeding ecology of the great tit (Parus major) in different habitats. Ardea 61:1-93.

van Balen, J.H. 1978. Population fluctuations, foraging and winter food. Progress Report 1977, Institute for Ecological Research, Arnhem. pp3-4.

Betts, M.M. 1955. The food of titmice in oak woodland. J. Anim. Ecol. 24:282-323.

Campbell,B. 1968. The Dean nestbox study 1942-1964. Forestry 41:26-46.

Charnov, E.L. 1976. Optimal foraging: attack strategy of a mantid. Amer. Nat. 110:141-151.

Charnov, E.L. and J.R. Krebs. 1974. On clutch size and fitness. Ibis 116:217-219.

Cody, M.L. 1974a. Optimization in ecology. Science 183: 1156-1164.

Cody, M.L. 1974b. Competition and the structure of bird communities.Princeton Univ. Press, Princeton, N.J.

Cohen, J.E. 1978. Food webs and niche space. Princeton, Univ. Press, Princeton, N.J.

Connell, J.H. 1975. Some mechanisms producing structure in natural communities: a model and evidence from field

experiments. Pages 460-490 in M.L.Cody and J.M. Diamond, eds. Ecology and evolution of communities. Harvard University Press, Cambridge, Massachusetts.

Dhondt, A.A. 1977. Interspecific competition between great and blue tits. Nature 268:521-523.

Dhondt, A.A. 1978. Interspecific competition in tits[reply]. Nature 275:463-464.

Dunn, E.K. 1977. Predation by weasels (Mustela nivalis) on breeding tits (Parus spp.) in relation to the density of tits and rodents. J. Anim. Ecol. 46:633-652.

Ford, H.A. 1979. Interspecific competition in Australian honeyeaters - depletion of common resources. Australian J. Ecol. 4:145-164.

Garnett, M.C. 1976. Some aspects of body size in the great tit. D. Phil thesis, Oxford Univ.

Gause, G.F. 1934. The struggle for existence. Williams and Wilkins, Baltimore, Maryland.

Geer, T.A. 1979. Sparrowhawk (Accipeter nisus) predation on tits (Parus spp). D. Phil thesis, Oxford University.

Gibb, J.A. 1953. Factors governing population density of birds of the genus Parus. D. Phil thesis, Oxford Univ.

Gibb, J.A. 1954. Feeding ecology of tits, with notes on treecreeper and goldcrest. Ibis 96:513-543.

Gibb, J.A. and M.M. Betts. 1963. Food and food supply of nestling tits (Paridae) in Breckland pine. J. Anim. Ecol. 32:489-533.

Grant, P.R.,B.R. Grant, J.N.M. Smith, I.J. Abbott and L.K. Abbott. 1976. Darwin's finches: population variation and natural selection. Proc. Nat. Acad. Sci. 73:257-261.

Green, R.F. 1979. A graph theoretical test to detect interference in selecting nest sites. Pages 439-452 in G.P. Patil and M.L. Rosenzweig, eds. Contemporary quantitative ecology and related econometrics. International Co-operative Publishing House, Burtonsville, Maryland.

Greenwood, P.J., P.H. Harvey and C.M. Perrins. 1979. The role of dispersal in the great tit (Parus major): the causes, consequences and heritability of natal dispersal. J. Anim. Ecol. 48:123-142.

Hamilton, T.H. and I. Rubinoff. 1967. On predicting insular variations in endemism and sympatry for Darwin's finches in the Galapagos Archipelago. Amer. Nat. 101:161-172.

Hartley, P.H.T. 1953. An ecological study of the feeding habits of the English titmice. J. Anim. Ecol. 22:261-288.

Higuchi, H. 1978. Use rates of nestboxes by birds according to forest types and the breeding density in forests with and without nestboxes. J. Japanese Forestry Service 60:255-261.

Hinde, R.A. 1952. The behaviour of the great tit (Parus major) and some other related species. Behaviour Suppl. 2.

Hogstad , O. 1975. Interspecific relations between willow warbler (Phylloscopus trochilus) and Brambling (Fringilla montifringilla). Norw. J. Zool. 23:223-234.

Högstedt, G. 1980. Prediction and a test of the effects of interspecific competition. Nature 283:64-66.

Horn, H.S. 1966. Measurement of 'overlap' in comparative ecological studies. Amer. Nat. 100:419-424.

Hutchinson, G.E. 1957. Concluding remarks. Cold Spring Harbor Symposium Quantitative Biology 22:415-427.

Källander, H. 1974. Advancement of laying of great tits by the provision of food. Ibis 116:365-367.

Kluijver, H.N. 1951. The population ecology of the great tit, Parus m. major L. Ardea 39:1-135.

Kluijver, H.N. 1952. Notes on body weight and time of breeding in the great tit, Parus m. major L. Ardea 40:123-141.

Krebs, J.R. 1970. Regulation of numbers in the great tit (Aves: Passeriformes). J. Zool., London 162:317-333.

Krebs, J.R. 1971. Territory and breeding density in the great tit, Parus major L. Ecology 52:2-22.

Lack, D. 1947. Darwin's finches. Cambridge University Press, Cambridge.

Lack, D. 1966. Population studies of birds. Oxford University Press, London.

Lack, D. 1969. Subspecies and sympatry in Darwin's finches. Evolution 23:252-263.

Levins, R. 1968. Evolution in changing environments. Princeton University Press, Princeton, N.J.

Levins, R. 1979. Coexistence in a variable environment. Amer. Nat. 114:765-783.

Lewontin, R.C. 1966. On the measurement of relative variability. Systematic Zool. 15:141-142.

Lotka, A.J. 1932. The growth of mixed populations: two species competing for a common food supply. J. Washington Acad. Sci. 22:461-469.

MacArthur, R.H. 1972. Geographical ecology: patterns in the distribution of species. Harper & Row, New York.

MacArthur, R.H. and E.O. Wilson. 1967. Island biogeography. Princeton University Press, Princeton, N.J.

May, R.M. 1974. On the theory of niche overlap. Theor. Pop. Biol. 5:297-332.

May, R.M. 1975. Some notes on the competition matrix, α. Ecology 56:737-741.

Maynard Smith, J. 1974. Models in ecology. Cambridge University Press, Cambridge.

Minot, E.O. 1978. Interspecific competition in tits. Nature 275:463.

Morris, R.F. 1959. Single-factor analysis in population dynamics. Ecology 40:580-588.

Morris, R.F. 1963. Predictive population equations based on key factors. Mem. Ent. Soc. Canada 32:16-21.

Morse, D.H. 1978. Structure and foraging patterns of flocks of tits and associated species in an English woodland during the winter. Ibis 120:298-312.

O'Connor, R.J. 1973. Growth and metabolism in some insectivorous birds compared with granivorous species. D. Phil. thesis, Oxford.

Orians, G.H. 1974. Diversity, stability and mortality in natural ecosystems. Pages 139-150 in W.H. Dobben & R.H. Lowe-McConnell, eds. Unifying concepts in ecology. Junk, The Hague.

Orians, G.H. and M.F. Willson. 1964. Interspecific territories of birds. Ecology 45:736-745.

Perrins, C.M. 1965. Population fluctuations and clutch size in the great tit (Parus major). J. Anim. Ecol. 34:601-647.

Perrins, C.M. 1966. The effect of beech crops on great tit populations and movements. Brit. Birds 59:419-432.

Perrins, C.M. 1970. The timing of birds' breeding seasons. Ibis 112:242-255.

Perrins, C.M. 1979. British tits. Collins, London.

Perrins, C.M. and D. Moss. 1975. Reproductive rates in the great tit. J. Anim. Ecol. 44:695-706.

Pianka, E.R. 1973. The structure of lizard communities. Ann. Rev. Ecol. Syst. 4:53-74.

Pianka, E.R. 1976. Competition and niche theory. Pages 114-141 in R.M. May, ed. Theoretical ecology. Blackwell Scientific Publications, Oxford.

Pielou, E.C. 1972. Niche width and overlap: a method for measuring them. Ecology 53:587-692.

Pielou, E.C. 1974. Population and community ecology. Gordon and Breach, New York.

Pielou, E.C. 1976. Ecological diversity. John Wiley & Sons, New York.

Poole, R.W. 1978. The statistical prediction of population fluctuations. Ann. Rev. Ecol. Syst. 9:427-448.

Reddingius, J. 1971. Gambling for existence. Acta Biotheoretica 20(suppl.).

Royama, T. 1959. A device of an auto-cinematic food-recorder. Tori 15:172-176.

Royama, T. 1970. Factors governing the hunting behaviour and selection of food by the great tit (Parus major L.). J. Anim. Ecol. 39:619-668.

Royama, T. 1977. Population persistence and density dependence. Ecological Monographs 47:1-35.

Schoener, T.W. 1974. Some methods for calculating competition coefficients from resource-utilization spectra. Amer. Nat. 108:332-340.

Shannon, C.E. 1948. A mathemetical theory of communication. Bell System Tech. J. 27:379-423, 623-656.

Shannon, C.E. and W. Weaver 1949. The mathematical theory of communication. University of Illinois Press, Urbana.

Slade, N.A. 1977. Statistical detection of density dependence from a series of sequential censuses. Ecology 58: 1094-1102.

Slagsvold, T. 1975. Critical period for regulation of great tit (Parus major L.) and blue tit (Parus caeruleus L.) populations. Norw. J. Zool. 23:67-88.

Southwood, T.R.E. 1976. Bionomic strategies and population parameters. Pages 26-48 in R.M. May, ed. Theoretical ecology. Blackwell Scientific Publications, Oxford.

Taylor, L.R. and I.P. Woiwod. 1980. Temporal stability as a density-dependent species characteristic. J. Anim. Ecol. 49:209-224.

Tinbergen, L. 1949. Bosvogels en insecten. Ned. Boschb. Tidschr. 4:91-105.

Tinbergen, L. 1960. The natural control of insects in pine woods. (i) Factors influencing the intensity of predation by song birds. Arch. Neerl. Zool. 13:265-343.

Tollanaar, D. 1922. Legperioden en eierproductie bij eenige wilde vogelsoorten, vergeleken met die bij hoenderrassen. Meded. Landb. Hoogesch. Wageningen 23(2):1-46).

Vandermeer, J.H. 1969. The competitive structure of communities: An experimental approach with protozoa. Ecology 50:362-371.

Varley, G.C. and G.R. Gradwell. 1960. Key factors in population studies. J. Anim. Ecol. 29:399-401.

Varley, G.C., G.R. Gradwell and M.P. Hassell. 1973. Insect population ecology. Blackwell, Oxford.

Volterra, V. 1926. Variatizioni e fluttuazioni del numero d'individui in specie animali conviventi. Mem. Real Accad. Nazionale Lincei 6(2):31-113.

Wangersky, P.J. 1978. Lotka-Volterra population models. Ann. Rev. Ecol. Syst. 9:189-218.

Webber, M.I. 1975. Some aspects of the non-breeding population dynamics of the great tit (Parus major). D. Phil. thesis, Oxford University.

Werner, E.E. 1976. Niche shift in sunfishes: experimental evidence. Science 191:404-406.

Wilbur, H.M. 1972. Competition, predation and the structure of the Ambystoma - Rana sylvatica community. Ecology 53:3-21.

Winkel, W. 1970. Experimentalle Untersuchungen zur Brutbiologie von Kohl- und Blaumeise [English summary]. J. Orn. 111: 154-174.

Wolda, H. 1978. Fluctuations in abundance of tropical insects. Amer. Nat. 112:1017-1045.