Some Aspects of Bill morphology in Relation to Ecology in the Great Tit Parus major.

by

A. Gosler
(Wolfson College)

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Edward Grey Institute of Field Ornithology,
Department of Zoology,
Oxford.

"It is a matter of curious enquiry to trace out how those species of soft-billed birds, that continue with us the winter through, subsist during the dead months."

Gilbert White 1775,
Letter XLI to Thomas
Pennant esq.

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Abstract.

Ornithologists have long recognised a relationship between bill morphology and the ecological niche between species. This general relationship was described for the genus **Parus** over 30 years ago. Recently, the long-held assumption that the relationship was adaptive in this genus (and in the Great tit in particular) has been questioned. This study examines the evidence that bill variation is adaptive (ie: contributes to fitness) in the marked Great tit population of Wytham Wood, Oxford, U.K.

Over 1000 full grown individuals were measured (mean retrap rate of 1.67 per bird) between May 1982 and July 1985. The short-term repeatability (which inversely measures observer error) for all measurements taken was over 90%. Bill characters were more variable than any other linear measurements taken. This was because bill characters varied strongly with sex (independent of sex-differences in body size) and season (within birds) and in males in spring, varied with age also. Long-term repeatability estimates were significantly lower than short-term, indicating that bill size changed between seasons (within birds). These results, together with a seasonal change in the heritability estimates of bill characters (which were greater in summer than in winter) indicated that they were strongly influenced by variation in the environment and that this was especially true in winter. Changes in adult bill size in spring were due to active bill moult. This has not been described previously in a passerine. The occurrence of moult was related to the bill size and behaviour of the bird and it was suggested that the bird might exercise some active control over the bill size.

Bill depth in 15 day-old nestlings was unimodal. Most of the explainable variation in bill depth at this age was due to variation in the growth environment. By four months of age, bill depth was strongly sexually dimorphic. Males had shorter but deeper bills than females. Evidence that this may have resulted from differential directional selection for bill depth itself is presented.

In general, there was little evidence for natural selection of or for bill characters in the birds once fully grown, but when observed, it tended to affect sub-dominant classes of birds. In winter, bill variation corresponded closely with variation in foraging niche among individuals. A series of laboratory experiments were carried out with captive birds to test their skill at handling different foods in relation to bill size. The differences in bill size and shape among age and sex classes observed in the field in relation to differences in niche corresponded with those expected from the optimal bill sizes (in terms of feeding efficiency) shown by the laboratory experiments. Other evidence was described to support the view that bill size and feeding efficiency were correlated. It was suggested that in winter, bill differences among age and sex classes allowed niche segregation within the population, so reducing intraspecific competition. In some summers, prey size correlated with bill length. In those summers, the mean fledging weight of chicks whose parents differed in bill length tended to be greater than that of chicks with more similar parents. It was suggested that this was because parents with different bill lengths competed less for food and so delivered more food to the nest.

The study concluded that bill size was highly adaptive in that it was related to fitness (in the broad sense) or to some correlate of fitness. The results are considered in terms of existing niche theory and especially of "character displacement" and the "variable niche hypothesis".

To my parents and Caroline.

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Glossary of bill terminology
and bill characters defined.

Glossary of bill terminology and bill characters defined.

Letters in parenthesis indicate the abbreviations used in the glossary diagram below.

Bill depth - (BD). Defined in text - the deepest point of the gonys anterior to the nares of the relaxed bill.

Bill length - (BL). Defined in text - chordal distance from the tip of the upper mandible to the base of the bill at the naso-frontal hinge of the skull.

Exposed Culmen - (BLe). Chordal distance between bill tip and feathering. In present study used for measurement of nestlings for whom measurement of bill length (above) might be dangerous.

Bill overlap - (Bo). Difference in length between the mandibles when relaxed.

Commissure - (Co). Point of contact of the mandibles (cf: tomia).

Culmen - (C). Dorsal ridge of the bill running from the skull to the tip.

Dertrum - the tip of the bill. Sometimes used specifically for a nail at the bill tip eg: in Anatidae.

Gnathotheca - (gn). Horny covering of the lower mandible (cf:rhamphotheca).

Gonys - (g). That part of the lower mandible where the rami are fused. In the Great tit, the proximal margin of the gonys marks the deepest part of the bill.

Nares - Nostrils.

Naso-frontal hinge - Point of contact between the proximal bones of the upper mandible and the cranium. Flexibility of the hinge allows a limited degree of elevation and depression of the upper mandible.

Rhamphotheca - (rh). The horny covering of the bill consisting of the gnathotheca and rhinotheca combined. That part of the bill which is continuously growing and which contributes most to the variance in bill size within individuals.

Rhinotheca - (r). Horny covering of the Upper mandible (cf:rhamphotheca).

Rictus - (ri). Angle of the bill formed by the connection of the mandibles at the proximal end of the commissure.

Rictal width - The width of the bill at the rictus, used mainly in pulli in the present study.

Rostrum - The bill in total, consisting of both skeletal components and the rhamphotheca.

Tomia - (t). Cutting edges of the mandibles. When the bill is closed, together forming the commissure.

Additional terms used.

Hard morphology - refers to characters showing little or no variation within individuals once full-grown, within the life of the individual. It is therefore appropriate for tarsus length (91.85% long-term repeatability) and other measurable skeletal dimensions.

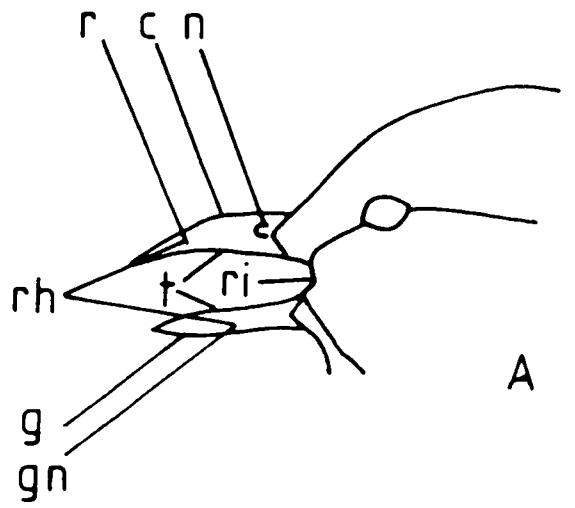
Immigrant - Used to denote an individual of unknown origin.

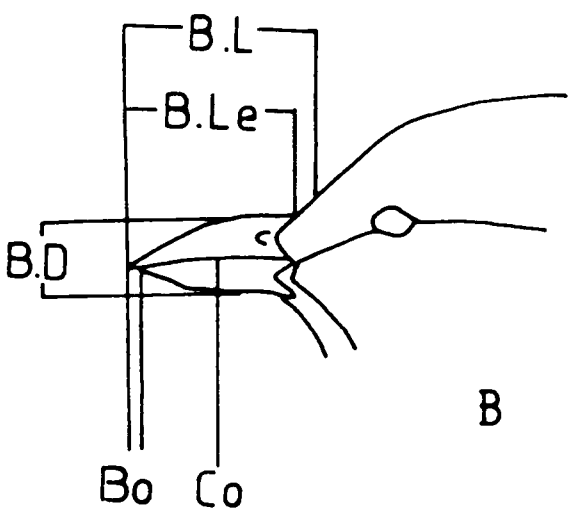
Resident - Used to denote an individual that is known to have been hatched within the Wytham study population.

Soft morphology - refers to characters showing marked variation within individuals once full-grown, within the life of the individual. It is therefore most applicable to fat score which shows marked diurnal and seasonal variation (66.98% long-term repeatability)

The terms hard and soft morphology reflect the long-term repeatability of

a character. Bill characters are intermediate in this nomenclature. Together with body weight, they show repeatabilities of 83-88% (see chapters 2 and 3).





GLOSSARY:

A. Terminology - c culmen, g gonys, gn gnathotheca, n nare, r rhinotheca rh rhamphotheca, ri rictus, t tomia.

B. Bill characters - BD bill depth, BL bill length, BLe bill length of exposed culmen, Bo bill overlap, Co commissure.

Chapter 1. Introduction and Aims.

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1.1 The ecological significance of bill variation. - A review.

It is an axiom of ornithology that gross bill morphology and the generalised niche are closely related in the higher taxa of birds (White 1789, Newton & Gadow 1896). However, it is only since the publication of 'Darwin's Finches' by Lack (1947) that the relationship has been recognised between congeneric species (Lack 1971, Ratcliffe and Boag 1983). Indeed prior to that it was generally believed that while morphological differences between genera were adaptive, those among congeners and infra-specific categories resulted largely from non-selective factors such as genetic drift.

Lack (1947) consolidated the ideas of Gause (1934), Grinnell (1943), Huxley (1942) and Mayr (1942) into what is now recognised as the 'competitive exclusion principle' (Hardin 1960). This states that two 'ecologically similar' species (often quoted specifically as congeneric species) cannot co-exist in sympatry. The commonest suggested cause for competitive exclusion is believed to be overlap in food requirements. Since bill morphology is clearly related to feeding ecology in the higher taxa, Lack reasoned the same for relatively subtle differences in bill-size and shape between congeneric species. He argued that bill-size should determine both the size of food items taken and the individual's ability to prepare such food. Hence interspecific differences in bill morphology could result from natural selection acting to reduce competition between related species by allowing them to exploit different ecological niches (Lack 1971).

Much research in the field of bird community ecology since 1947 has attempted to validate Lack's ideas. However, as Hespenheide (1973) has pointed out, few of these studies have attempted to show a relationship between bill-size and resource utilisation. Lack assumed (without evidence) that such a relationship must exist. This assumption has become universally accepted (until recently) but it has remained a central tenet of bird community ecology without formal demonstration for most taxa. Further, many studies have been based solely upon measurements of museum specimens. They have frequently used series from a wide geographical range without due consideration for clinal, age-specific, sex-specific or seasonal variation in the characters investigated (see for example Davis 1954, Van Valen 1965, Johnson 1977, and Willson 1975). Hence much previous work in this area of systematic ecology may be invalidated by more stringent field studies. It should be stated that the evidence for the competitive exclusion principle may suffer from circular reasoning. For example, if we notice that congeneric species always differ in their ecology we cannot attribute their coexistence to differences in morphology since without any such differences we should be unable to describe them as different species. The hypothesis is supported however, if congeneric species differ more in sympatry than they do in allopatry.

In 1956, Brown and Wilson suggested the term 'character displacement' to describe the morphological separation of ecologically similar species in sympatry. Character displacement was implicitly related to the process of competitive exclusion described by Lack. It was quickly taken up by community ecologists such as Hutchinson (1959) and MacArthur (see MacArthur and Wilson 1967) seeking to explain patterns of species diversity in terms of niche ecology. Hutchinson (1959) suggested that a minimum similarity in trophic

characters (such as bill length - see glossary) existed in sympatric congeners within which coexistence could not occur. This was reflected in the general observation that in comparisons of pairs of sympatric congeneric species, the ratio of measurements of such characters lay consistently between 1.2 and 1.6. That is, the larger was between 1.2 and 1.6 times greater than the smaller. This concept of minimal similarity seemed also to be supported by theoretical studies in community ecology suggesting that a minimum niche overlap giving a ratio of about 1.3 of mean resource utilisation should be expected for two species distributed along a resource gradient (May and MacArthur 1972). By assuming a perfect mapping of bill-size onto this resource gradient, this agreed well with 'Hutchinson's principle'. Simberloff and Boecklen (1981) have pointed out that random comparisons of congeneric species, whether sympatric or allopatric, also give ratios of the order described by Hutchinson, and suggest that:

> ..."In no sense is the "1.3 rule" of size ratios a rule of nature; even published results tend to support it weakly at best, and negative results are probably less frequently reported."...

Indeed, from a taxonomic viewpoint, recognising such taxa as distinct species but within a genus in the first place, constrains the possible range of such ratios. Simberloff and Boecklen (1981) concluded:

> "We do not claim that sizes are not partly determined by competition, nor that our hypothesis of independent, random sizes is correct. But we do feel that the evidence presented to date that sizes are competitively determined is weak, and that in particular the "1.3 rule" was probably always a red herring and has certainly outlived its usefulness to evolutionary ecologists."

Recent work, particularly in Europe and the Galapagos archipelago has been more rigorous. Emphasis has at last been placed on the need to determine the extent of niche-overlap between species along defined resource dimensions, and to determine empirically the relationships among bill size, prey size, handling and selection (Ashmole 1968; Holmes and Pitelka 1968; Newton 1972; Williams and Batzli 1979a, 1979b; Grant 1981; Boag and Grant 1981; Fjeldsa 1981, 1982, 1983; Carlson and Moreno 1983; Paszkowski and Moermond 1984).

Grant (1972) has pointed out that many of the examples of character displacement cited by Brown and Wilson (1956) are open to explanations other than competitive exclusion, and has redefined character displacement strictly in terms of a competitive process :

> "(Character displacement is...) the process by which a morphological character state of a species changes under natural selection arising from the presence, in the same environment of one or more species similar to it ecologically and/or reproductively."
>
> Grant (1972)

Grant states that the antithesis of character displacement is character release. This may be similarly defined except that selection arises in this case through the disappearance of a formerly competing sympatric species which had caused the displacement of a character. Together, character displacement and character release constitute a character shift.

Grant (1975) has pointed out that the evidence for character displacement resulting from competitive exclusion is pitifully inadequate. He suggested that although Bulmer (1974) had shown that the process was possible mathematically, it was equally likely that apparent examples of character displacement simply reflected 'workable combinations' of species, that is, species that differed sufficently due to the fortunes of speciation in isolation might coexist, those that do not - cannot.

Much of the research on the relationship between food and bill morphology (particularly with respect to size) has been concerned with granivorous species. Morris (1955), Bowman (1961), Kear (1962), Hespenheide (1966), Newton (1972), Willson (1972) and Grant (1981) have all demonstrated a positive correlation between bill depth and/or length and the size (and hardness) of seed preferred by a variety of finch species. However, although a positive correlation between bill length and prey size has frequently been assumed for insectivorous species (Hespenheide 1971, Schoener 1971b, Willson et al. 1975, Greenberg 1981) it has rarely been demonstrated empirically (but see Lederer 1975) for each species considered. Indeed there is evidence that in some insectivorous passerines a negative correlation between prey size and bill length may occur (Hespenheide 1973) and several authors point out that it is the variance rather than (or in addition to) the mean of prey size that may increase with an increase in bill length (Grant 1968, Hespenheide

1973, Wilson 1975, Herrera 1978a).

Schoener (1965), Grant (1967), Soulé and Stewart (1970), Hespenheide (1971) and Willson et al. (1975) have all used bill length as the ecologically segregating character in their analyses of niche separation across a wide range of passerine species. Clearly there are dangers in this, especially when it is assumed that bill length is as valid a character in segregating species in the Hirundinidae (swallows) as in the Tyrannidae (New-world flycatchers) and Vireonidae (vireos) (Hespenheide 1971). It is perhaps not surprising that Hespenheide concluded, on the basis of such an analysis, that body size was a better predictor of prey size than was bill length amongst such a diverse assemblage.

The development of foraging theory has allowed some general predictions to be made concerning the relationship between bill morphology and feeding ecology (Schoener 1971a). Ultimately these relationships might be predicted by the abundance of food available to a particular foraging guild (sensu Root 1967). Schoener (1971a) pointed out that the total foraging-time of an individual (T) can be divided into time spent searching for prey (t_s) and time spent handling prey (t_h) (including both selecting and processing a prey item), such that:

$$T = t_s + t_h$$

In this model, if a greater part of the time is spent searching, (as when food is scarce) less time is available for handling, and especially for prey selection since processing time might be less easily reduced. If food is abundant, search time is reduced and the animal is free to feed selectively - or to quote Root (1967) 'optimising its food consumption within its morphological mode'. The essential assumption of this model is that total

foraging time is constant. This assumption is easily violated if total foraging time may be increased by reducing the amount of time spent in some other activity such as preening or territory defence. Hence, the assumptions of this model are met most closely when most of the animal's time is spent in foraging such as on extremely cold days in winter, or when feeding a large brood of chicks.

Following the predictions of the Schoener model, when food is abundant animals might be expected to specialise and when it is scarce they should generalise. Although there may be theoretical objections to the Schoener model other than that mentioned above, this simple prediction is also supported by more recent work on optimal foraging and 'spreading risk' (see Lendrem 1986 for a brief review). It follows also from niche theory (Hutchinson 1957) that within the constraints of community structure, generalist foragers should occupy a broader realised specific niche than specialist foragers. If bill morphology is adaptive it may reflect the foraging strategy employed. This view of foraging strategy in relation to food availability is supported by the observations of a number of authors (MacArthur and Pianka 1966, Schoener 1971b). In its original form, Schoener's model predicts that bill differences between species that reflect different specialisations within a niche dimension might occur only when food was abundant, but when competition should be least effective. Smith et al. (1978) have modified the basic argument to allow for character displacement (sensu Grant 1972). They suggest a "U" shaped function relating food abundance to a gradient of foraging strategy from generalist to specialist. In this model animals specialise when food is superabundant (due to the reduction in search time), generalise when food is moderately available (due to the increase in search time), but specialise again to reduce interspecific competition when

food is very scarce (by selecting food within the morphological constraints set by character displacement resulting from competition for food). Within this generalised framework, it is not possible to provide an a priori quantification of food abundance (ie: no definition of "superabundant" etc.) since it must reflect not only the abundance of food, but also the size and density of animals feeding upon it.

Hespenheide (1973) has augmented this model by suggesting a mechanism whereby character shift might occur when food is superabundant. He considers the case of two species with normally distributed, overlapping resource utilisation curves. Both curves lie well within a curve of resource availability such that more food is available at one end of the resource gradient. That is, the utilisation curves of the two species do not lie symmetrically within the curve of availability. For the sake of argument, more food is available towards the upper end of the resource gradient. The species with the greater mean of resource utilisation (that is, the species whose mean lies closest to the upper end of the overall resource distribution) would shift its mean to take advantage of this under-utilised portion of the resource. If the resource gradient is prey size, and if bill size is correlated with prey size, larger individuals may have an advantage over smaller conspecifics whose utilisation curves still overlap that of the other species. Since failure to shift the mean would not reduce the intrinsic rate of natural increase of either population, he considers this process distinct from character displacement due to competitive exclusion, but still leading to a shift in the mean bill size due to differential production of offspring (fitness sensu Endler 1986) within the population. He terms this scenario character displacement (shift) by under-utilisation to distinguish it from the competitive process which he terms character displacement by over-

utilisation.

Levins (1968) has applied the basic generalist/specialist model to the question of environmental predictability. By extrapolation, an animal in an unpredictable environment should be more generalised in its foraging. If food is predictable, the animal may be more specialised. These predictions should be superimposed upon those relating foraging strategy and food abundance since food may be either predictable or not and of either high or low abundance. Fretwell (1978) has argued that a discrete distribution of resources (such as prey type) favours a generalist strategy while a continuous distribution (such as prey size) favours specialisation.

There is now an extensive literature concerned with character displacement. It has been advocated as an explanation for patterns of variation in a wide range of bird taxa (see the major review by Lack 1971), in Honeycreepers (Drepanididae) by Bock (1970), in Grebes (Podicipedidae) by Fjeldsa (1981,1982,1983), in Wrens (Thryothorus) by Grant (1966), Chaffinches (Fringillidae) by Grant (1979), in Flycatchers (Tyrannidae) by Hespenheide (1971) (although Johnson (1966) suggested that there was no evidence for displacement in this family), and, as will be shown in the next section, in Tits (Paridae) (see Alatalo 1982 for a review). Despite the widespread use of character displacement to explain morphological variation, it should not be seen as a panacea for problems in eco-morphology. Wiens and Rotenberry (1979) studied the diet/niche relationships amongst a large number of bird species in grassland and shrub-steppe habitats in North America. They found large overlaps in niche between these species. Further, they found no correlation between prey size and either bill size or body size, although larger species tended to take a greater variance of prey size. On average, each individual took 30-40% of the total available prey types.

Food ranged in availability from unpredictable and scarce, to very abundant and predictable so that most species were opportunistic generalist foragers. This may explain the lack of correlation between ecology and morphology. They suggested that their inability to show clear relationships in accord with usual ecological theory was due both to a lack of data on the resource bases, and to their lack of suitable hypotheses to test patterns of community structure and organisation. They concluded that "We suggest that these complications may compromise the findings of many community studies".

Mention should be made of the phenomenon of character convergence. This is found in similar species which segregate ecologically by defending mutually exclusive territories rather than by differences in morphology (Cody 1969). In this case, selection favours the convergence of behaviourally segregating characters such as song and plumage marks which facilitate interspecific recognition of territorial boundaries (Cody 1969). Such a system is seen in Wheatears (Oenanthe) (Streseman 1950) which differ little in bill morphology between species (Potapova and Panov 1977). Ashmole (1968) pointed out that the lack of character displacement observed among Empidonax spp. by Johnson (1966), (and mentioned above) was due to their interspecific defence of mutually exclusive territories. Cody (1973) has attempted to explain why some species are ecologically segregated by morphology while others are segregated by behaviour in this way. He proposed a similar model to that later described by Smith et al. (1978) and described here above. This model relates food abundance to a gradient from character convergence to divergence by an inverse "U" shaped function. Hence when food is neither superabundant nor very scarce, (a situation favouring generalisation) character convergence and interspecific territoriality should occur. Fig. 1.1 presents the theories of Smith et al. (1978) and Cody (1973) in graphical form. Schoener

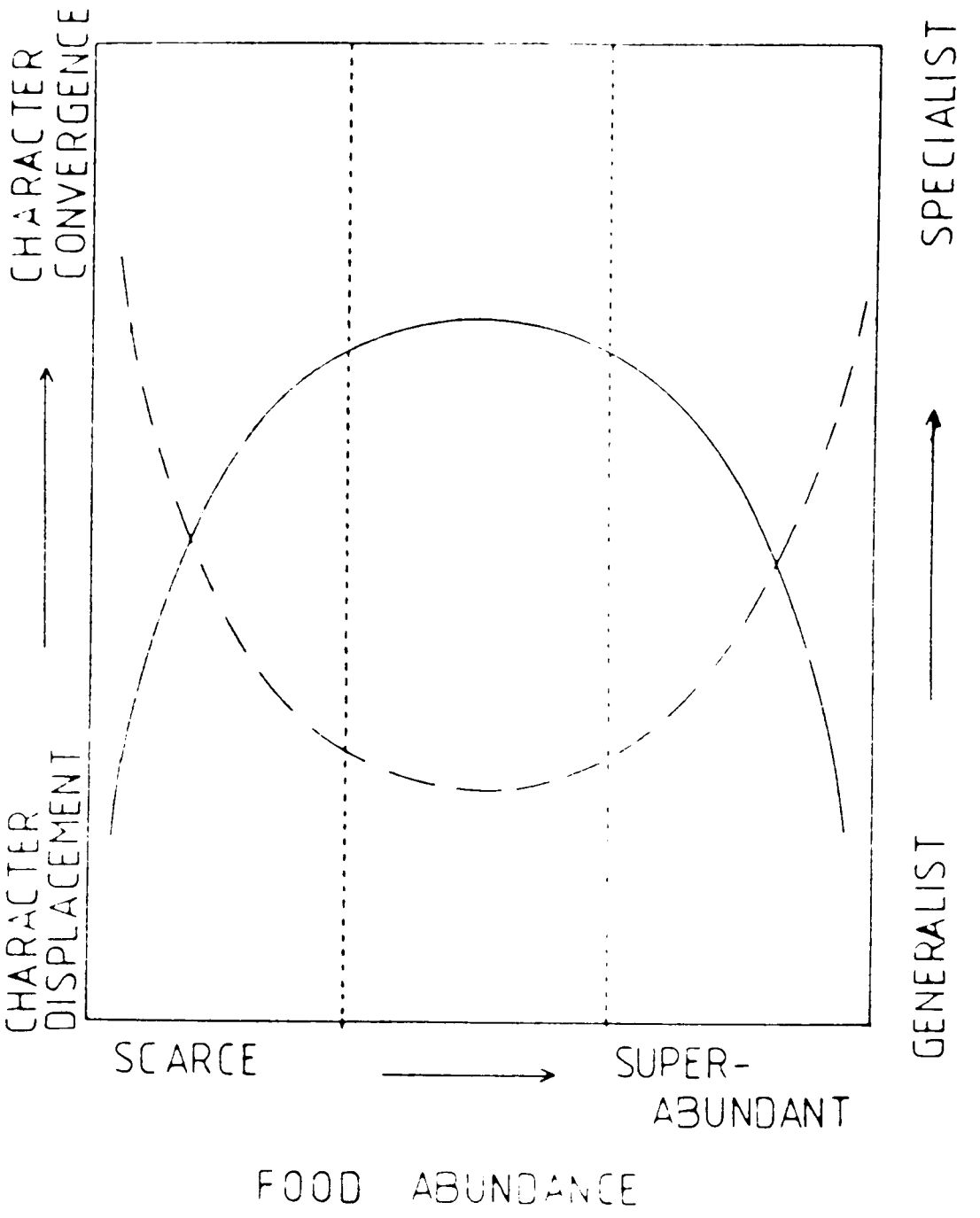


Figure 1.1. A diagramatic representation of the relationships between character displacement/convergence and food abundance indicated by the solid line (based on Cody 1973) and Generalist/specialist foraging and food abundance indicated by the dashed line (based on Smith et al. 1978). The model suggests that character displacement, associated with dietary specialisation occurs both under conditions of food scarcity and super-abundance. At intermediate levels of food availability, character convergence and dietary generalisation are observed.

Schoener (1965) also considered this problem and suggested that the solution favoured (character displacement or interspecific territoriality) might depend upon the number of species involved:

(1) Few species = specialisation on different sizes of the same food type = Character Displacement

(2) Many species = Avoid competition by differing in feeding habitat, behaviour or by defending exclusive territories. = Character Convergence

Again, no a priori judgement of what constitutes "few" or "many" species is possible, since it must depend upon the niche ecology of the taxa involved.

It has often proved difficult to apply these various models to specific cases. For example, warblers of the genus Sylvia not only aggressively defend interspecific territories and show song convergence (Garcia 1983), but also show considerable morphological and ecological differences between species (Mason 1976). The same may be true of the Acrocephalus warblers, although the situation is further complicated in this group by the occupation of non-feeding territories (Catchpole 1973, Winkler and Leisler 1985, Shennan 1985). These apparent contradictions to the predictions of the models arise partly from the seasonal variation of food supply (type, quality and abundance). For example, as Hespenheide (1973) has pointed out, selection for bill size and shape through character displacement will occur when competition for food is most intense, perhaps in the winter. Hence no relationship might be found between bill morphology and ecology when these pressures are relaxed. In the warbler examples, most of the species in Western

Europe are migratory, most populations wintering south of the Sahara in Africa. Hence in winter, these individuals experience competition from a range of species and on a range of resources not encountered in summer.

The importance of intraspecific bill variation.

It should be clear from this preamble that most previous work attempting to validate Lack's general thesis of ecological isolation in birds has been made by interspecific comparison. The warbler examples above highlight some of the dangers involved in interspecific comparison in eco-morphology. Principally, there may be unrecognised variables which are specific to the phylogenetic history and/or ecology of a particular taxon, and which confound a comparison between ecology and morphology between species. Since it is individuals rather than larger taxonomic groups which are selected (Endler 1986) more understanding should be gained by comparison of ecology and morphology within species. Chief amongst the advocates of this approach has been Grant and his co-workers studying the Geospizine finches of the Galapagos archipelago.

The analysis of intraspecific bill variation requires a more detailed understanding of variation within the specific niche. Christiansen and Fenchel (1977) considered the total niche width as a total variance measure (V_t) broken down into a series of variance components. They recognised a "within phenotype" component (V_w), a "between phenotype" component (V_b) and an age-specific component (V_a) so that:

$$V_t = V_w + V_b + V_a.$$

Taking this approach further, we might recognise a sex-specific component of niche variation as that part of the niche variance which is not already explained by the within or between phenotype components. The whole system may be subject to seasonal change as the availability of niches change through the year and as Christiansen and Frenchel point out, each component may itself contain both a genotypic and an environmental component.

The concepts of age- and sex-specific niche allow direct comparison with age- and sex-specific variation in bill morphology within a species. This is comparable with interspecific analysis but here, age and sex classes are used instead of different species. Hence the analysis of character variation in relation to competitive exclusion may be carried out at the intraspecific level. Now, in a social species, intraspecific behavioural dominance and competition become the agents of competitive exclusion, rather than interspecific competition. Morse (1974) has pointed out that in such a system, behavioural dominance may determine both the availability and the predictability of food. A direct comparison with the interspecific model (of Levins 1968) is then possible. Since food is more available, and access to food more predictable to dominant individuals, they should be more specialised in their foraging. In contrast, subdominants have less access to food and should be more generalised in their diet. The behavioural corollary of a generalist diet is opportunism (Morse 1970, 1974).

The analysis of intraspecific variation and ecology is not perfectly analogous to the interspecific case. In interspecific competition, the competitive exclusion principle predicts that one species should go extinct when in sympatry in the absence of ecological segregation (Hardin 1960). This clearly cannot occur within species where intraspecific competition is mediated by age or sex differences since the birds share 'common interests'

related to their own fitness. For example, males may dominate females, and even partially exclude them from resources, but it is not in the 'interest' of males to exclude females to the point of extinction since their own fitness (in terms of number of offspring produced) would suffer! However, it is still valid to argue that character displacement between sexes or age groups might evolve to reduce the intensity of such competition within species.

Van Valen (1965) made the logical connection between niche breadth and the extent of bill variation within a species. He pointed out that a species might occupy a broad realised niche by one of two strategies. First, by generalist foraging - in which all individuals forage in a generalist manner. Secondly, by specialist foraging in which the different members of the population each specialised on a different but restricted part of the specific niche. Such differential niche occupancy within a species may arise from differences between age classes (eg: Pollis 1984) or between sexes (Willson 1969 and see chapter 3) and might result from intraspecific competition mediated by social dominance (Morse 1974). Van Valen suggested that the morphological corollary of such niche variation should be manifest in one of two ways. In the first case (generalised foraging), by the evolution of a "general-purpose bill" (see Fjeldsa 1983 for an example) but with no predictable effect on bill variation within the species. Hence in such species a broad niche would not correspond to a high coefficient of variation for relevant bill characters. In the second case (specialised foraging), by increased variation in those trophic characters most concerned with the specialisation of diet. This has become known as the "Variable Niche Hypothesis". Van Valen tested his hypothesis by comparing the variance in bill length amongst series of skins from island and mainland populations of the same species. Only species (6 in all) in which a greater niche breadth on islands had been reported in the

literature were used. In all cases, he found that bill length was more variable in the island populations, despite the wide geographical area from which the continental 'population' had been drawn. Again, it was assumed (without test) that bill length was a relevant character in each case. Crowell (1961,1962) had effectively already carried out this analysis on three species on Bermuda. He found no difference in the amount of variation in the bills of these species when compared with mainland populations of the same species although all showed greater niche breadth on the island. Grant (1967) presented similar data offering "inconclusive support" for the variable niche hypothesis, and suggested that a high relative variance in bill characters represented a 'Jack-of-all-trades' foraging strategy.

Soulé and Stewart (1970) tested the variable niche hypothesis by comparing the bill variation of generalist foragers (crows) with that of a number of specialist foragers and naturally found no 'evidence' to support the hypothesis. Van Valen and Grant (1970) were quick to point out (or rather reiterate) that the variable niche hypothesis predicts an increase in bill variation only when the specific niche is broadened by differential sub-niche specialisation within the total niche. In short, Soulé and Stewart attacked the variable niche hypothesis with an irrelevant analysis.

Willson (1969) and Willson et al. (1975) also found little evidence to support the variable niche hypothesis in a series of gross comparisons among more than 1000 skins of 55 North American species. These analyses are to some extent open to the same criticism that Van Valen and Grant levelled against Soulé and Stewart. I shall discuss them later since they mainly concern sexual dimorphism. Rothstein (1973) found evidence in support of the hypothesis in a more rigorous series of tests than were performed by either Soulé and Stewart or Willson et al. First, he suggested that abundant species which occupied

broad niches in a community should show greater bill variation than rarer species with broad niches in the same community. He reasoned that common species would experience more intraspecific competition than rarer species. Hence common species were more likely to show intraspecific niche segregation. To test this he examined fifteen passerine species on the Trés Marias islands and found that common species were significantly more variable in bill characters than the rarer species. Secondly, he argued that the niche breadth (and therefore the coefficient of variation of bill characters) should be inversely proportional to the degree of sympatry and therefore the intensity of interspecific competition. He defined the degree of sympatry as the percentage of random locations shared by two congeneric species. He found that congeneric species which occured more frequently in sympatry were significantly less variable in bill length, width and in tarsus length than those which were less often found in sympatry. Further, in two genera, the increased morphological variation observed in allopatric species was due to an increase in the amount of sexual dimorphism. He concluded that under the conditions originally described by Van Valen (1965) and re-stated by Van Valen and Grant (1970), bill variation was significantly greater in species occupying broader niches. Further, that this increased variation was due to discontinuous variation in the population such as age and sex differences rather than resulting from selection for high phenotypic variance itself.

Evidence in support of the variable niche hypothesis remains weak, and at its best is only circumstantial. Hespenheide (1973) pointed out that it had never been tested within a live population of birds. This remains true although some indication of its validity in the Oystercatcher Haematopus ostralegus was implied by the work of Swennen et al. (1983) and Hulsher (1985). The variable niche hypothesis implies that small differences in bill

size and or shape among individuals correspond to small differences in niche. That is, bill morphology is intimately related to ecology at the level of the individual. Some evidence in support of the hypothesis is presented in the present work.

The field of theoretical avian community ecology suffers from a relative lack of work carried out on live birds. The literature is replete with hypothesis testing by reference only to museum series (most of the references cited in the last five paragraphs), and by the measurement of characters which may be irrelevant to the ecology of the species concerned. For example, might not gape width be more important than bill length in swallows? yet several studies consider only bill length in comparisons across several taxa including Hirundinidae (see Hespenheide 1971). Despite Ludicke's (1933) demonstration that the rhampotheca undergoes continuous growth and wear, and that the growth rate of the passerine bill is a function of the rate of loss, no workers in the 'comparatve school' give more than a passing acknowledgement of the dynamic nature of the bill. Hence the potential which exists for seasonal change in bill size in concert with seasonal shifts in diet and niche is all but ignored.

With the possibility of phenotypic plasticity in bill characters, character displacement need not be viewed only in terms of changes in gene frequencies within populations brought about by natural selection over many generations as is usually implied. It can occur within cohorts and within a generation through direct interaction with the environment but it must be the environmental component of phenotypic variance (rather than the genetic) that is involved in such a character shift. Until this study, this had been demonstrated for one species only. Swennen et al. (1983) and Hulsher (1985)

showed in the Oystercatcher that the size and shape of the bill changed predictably within individuals with a change in diet and feeding method. This change was largely caused by a change in the relative importance of growth and wear on the bill and allowed a greater feeding efficiency on the new food than was possible without modification of the bill. Further, differences in bill form corresponded with differences between age and sex classes.

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1.2 Bill variation and niche ecology in *Parus*.

I have deliberately delayed presenting examples from the genus *Parus* in support of Lack's thesis until now. Lack himself considered that the European tits (*Parus* spp.) offered "a complex example of coexistence" (Lack 1971) in which up to seven resident, congeneric species might occur sympatrically.

Parus is a genus of small passerines (in Europe ranging from 8 - 20 g in weight) occurring in a range of habitats, but showing a preference for woodland. Two species, the Coal tit *P. ater* and the Crested tit *P. cristatus* prefer coniferous woodland. However, (in Britain at least) the former also occurs in deciduous woodland and its numbers are correlated across winters with the quality of the beech mast crop (Glue 1982). A third species, the Willow tit *P. montanus* is probably limited by the abundance of dead tree stumps in which it excavates its nest chamber (Perrins 1979, Gosler 1986). In Britain it is therefore restricted to damp woodland. In continental Europe it is common in coniferous woodland. Its sibling species, the Marsh tit *P. palustris* is more strictly a bird of deciduous woodland. The Blue tit *P. caeruleus* and the Great tit *P. major* are the most cosmopolitan of the tit species in Britain and across much of Europe. Both breed in a wide range of woodland and suburban habitats although for both, mature oak (*Quercetum*) woodland is optimal (Van Balen 1973).

The tits are essentially insectivorous but all take a variable proportion of vegetable food in the diet, especially in winter when invertebrates are least abundant. This propensity varies between species and locations but is most pronounced in the Great tit. The population dynamics and movements of this species are partly related to the quality of tree seed crops in winter

such as Beech Fagus sylvatica and Hazel Corylus avellana (Perrins 1965, 1966). The Blue, Marsh and Coal tits may also concentrate their foraging on beech mast when it is plentiful. When food becomes scarce in winter, tits form mixed-species flocks of up to 100 individuals (see Morse 1978). These flocks are highly mobile and probably increase each individual's chance of finding food and detecting predators (Krebs et al. 1972, Krebs 1973). Mobile mixed-species flocks with some group integrity should not be confused with temporary aggregations of tits at an abundant local food source such as when a good beech crop is available. Several hundred Great tits may be present on the latter occasions (Perrins 1979 and own observation). In flocks the Great tit occupies perhaps the broadest niche (Gibb 1954). However, where food is abundant (such as during a good beech crop) it specialises on that food.

In summer, the breeding season is timed to coincide with the peak abundance of caterpillars (Lack 1966; Perrins 1970, 1976) which form the bulk of the food fed to the young (Royama 1966). The high abundance of food in many woodland habitats in summer is thought to be the reason for the large niche overlap between many species (including all the tit species) at this time (Hartley 1953, Gibb 1954, Betts 1955, Minot 1981). Niche differences among the tits are more evident in winter, and show variation between winters due to changes in the quality of seed crops. When mast is available, Great tits feed more on the ground, concentrating on this resource more than do the other species (Hartley 1953, Gibb 1954). Niche differences among the tits in winter have been defined in terms of feeding height (Hartley 1953, Gibb 1954, Snow 1953, 1954, and Betts 1955), feeding station (Hartley 1953, Morse 1978), and food type and size (Betts 1955). To this should be added feeding method which is the behavioural corollate of these ecological distinctions. Variations in body size, wing length , tarsus length, bill length and depth reflect

differences in these various niche dimensions (Snow 1953, 1954).

Lack (1971) found that in Europe there are rarely more than six Parus species occurring in sympatry. Herrera (1981) studied the Parus communities in each of 88 locations and ranked the species in order of their relative frequency or ubiquity. The Great tit was found in nearly all of the sites, irrespective of the number of species present at the site. This was closely followed by the Blue tit, and then the Marsh tit and Willow tit. The Crested and Coal tits were the least widespread. However, in most communities containing five species, Crested and Coal tits usually replaced Marsh or Willow tits. These analyses demonstrated that the associations of species present in Parus communities were not random. Instead, they reflected both the adaptability (in terms of the number of habitats occupied) and the relative dominance (in terms of social and ecological competitive ability) of the species.

The dominance of the Great tit over other Parus species is also reflected in work by Snow (1949). He found that in winter flocks dominated by this species in Sweden, Crested and Willow tits fed lower in the woodland profile than when Great tits were absent. Snow suggested that this reduced their niche overlap with the Great tit, so reducing competition. Niche shifts of this kind give the strongest evidence for competitive exclusion among tit species (Diamond 1978, Alatalo 1982). In Norway, Hogstad (1978) found that Willow tits expanded their potential niche overlap in coniferous forest in the absence of Crested tits in winter. These studies agree with the general observation of Morse (1970, 1974) that sub-dominant species occupy a broader fundamental niche (sensu Hutchinson 1957) and are more generalised in their foraging than the more specialised dominant species. Morse suggests that this observation contradicts the expected pattern of niche breadth predicted by a

'between-species' dominance hierarchy mediated by body size as in Parus (Perrins 1979). He says that this is because if the variance (breadth) of a niche dimension such as prey size increases with body size (as suggested by Hespenheide 1971), the smaller sub-dominants should occupy a less varied niche. However, niche breadth is rarely expressed in terms of prey size in Parus, but rather in terms of the relative frequency of feeding observations at different feeding stations (see above). There is no a priori reason for equating differences in niche breadth among species expressed in these terms with differences in body size. Having said this, Morse's explanation for the inverse relationship between realised niche breadth and dominance rank agrees with the preceding argument. That is, dominant species occupy a more predictable niche than sub-dominants. Dominants therefore specialise in their foraging whilst sub-dominants generalise. In an attempt to reduce competition with dominants, they become opportunists, so reducing their overlap in niche rather than niche breadth itself. It is not clear why they do not specialise when in allopatry. Perhaps, following the analyses of Herrera (1981) described above, the lack of a dominant Parus species indicates something about the habitat itself which demands generalised foraging (eg: low food abundance).

Alerstam et al. (1974) compared the tit communities on the Swedish island of Götland with those on mainland Scania. They found that the highly sedentary Willow, Marsh and Crested tits were absent from Gotland (see Sellars 1984 for an analysis of movements of British populations of these species). The foraging niches of Great and Blue tits were un-modified on the island, but the Coal tit fed in a significantly broader niche there. They suggested that the Coal tit reduced its niche breadth in the presence of Crested and Willow tits. In this case, the niche breadth itself was reduced in sympatry. The difference

in body weight between these species is far less than between those quoted above in which the Great tit is the dominant species. Hence it is possible that this niche variation resulted from diffuse competitive exclusion rather than direct dominance interactions.

Drawing together these examples, two kinds of shift in winter foraging niche might be defined in Parus in Europe:

(1) BEHAVIOURAL SHIFT. Niche shifts in the presence of a behaviourally dominant competitor where the realised niche of the subdominant is broader than that of the dominant. This results from a difference in foraging strategy (generalist/specialist). Here niche overlap rather than niche breadth is minimised by the sub-dominant. Might also be termed an ENVIRONMENTAL SHIFT.

(2) SELECTIVE SHIFT. Niche shifts in the presence of a congener of similar competitive ability where indirect or diffuse competition may cause a reduction in niche breadth and/or location in one or both competing species. Here niche breadth is minimised by a shift in location which may cause a reduction in niche breadth. Might also be termed a GENETIC SHIFT.

These are not mutually exclusive. Either, or both might occur in any community. The behavioural shift is principally a temporary event - an environmental effect acting only upon the environmental component of phenotypic variation. The selective shift results from sustained

competition, leading to a shift in gene frequencies by natural selection for character states which allow coexistence through niche shift. Hence it is the latter form of niche shift that is principally considered to lead to character displacement between species. However, intraspecific behavioural dominance may itself constitute a sustained competitive effect within species.

Alatalo (1982) has reviewed the evidence for interspecific competition among European tit species. He concludes that niche shifts of the kind quoted above give the strongest evidence for interspecific competition in winter. Despite the many studies of niche differences in Parus, few have considered the morphological corollary and especially the evidence for character displacement, although it is frequently implied (Lack 1971). Herrera (1978b) compared two communities of tits in "identical" habitat in southern Spain. The first contained Great, Blue and Crested tits. The second lacked the Crested tit. In allopatry, he found that the Blue tits were identical to the Crested tits in bill length. In sympatry with the Crested tit however, the Blue tit shifted its niche (defined as the relative time spent at each of a series of feeding stations) away from that of the Crested tit, and showed a significant reduction in bill length. The Great tit niche differed from those of the other two species both in sympatry and in allopatry. No difference in either niche or bill length was observed in the Great tit between sympatric and allopatric populations.

Following the demonstrations by Hartley (1953) and Gibb (1954) that British tits in deciduous woodland occupied different feeding stations; Betts (1955) examined the food of tits in oak woodland. She then related the results of this study to differences in morphology amongst species. She found positive correlations amongst body size, bill length and prey size (estimated from gut content) among species. However, she did not correlate bill size,

body size and prey size within species. Implicit in many of the "classical" studies of tit niche ecology is the assumption that because food is relatively scarce in winter and temporarily "superabundant" in summer when the birds breed (Perrins 1970, 1979) niche segregation due to competition should be strongest in winter. Hence character displacement by over-utilisation is implied and character differences among species (at least in bill size) are thought to be relatively unimportant in summer (Lack 1971). Indeed, Gibb (1954) and Betts (1955) point out that niche overlap is greatly increased in summer (but see Ulfstrand 1977). However, recent studies in Belgium (Dhondt 1977, Dhondt and Eyckerman 1980) and Britain (Minot 1981, Minot and Perrins 1986) suggest that competition for food between Great and Blue tits in summer is not insignificant. Minot (1981) found that the presence of Blue tits in an area significantly reduced the mean fledging weight (a correlate of chick survival, Perrins 1963, 1965) of Great tits. Great tits had no effect on Blue tit weight. Although not considered by Minot, it is possible that since Blue tit chicks hatch on average about a week before Great tits (Dunn 1976) the smaller Blue tit parents took younger members of the same caterpillar species that would later be taken by the larger Great tit parents. That is, the difference in body and bill size between the two species meant that Blue tits fed their young partly on 'incipient' Great tit prey. The difference in date between the two species, caused by the difference in body size (Dunn 1976, Perrins 1970) would make it impossible for Great tits to compete by morphological character displacement.

The functional relationship between bill size and prey size has not been established for any tit species. Snow (1953, 1954) found that within several Parus species, bill length decreased with increasing latitude in accordance with Allen's rule. He also showed that species with a preference for

coniferous woodland had relatively long, thin bills whilst those preferring deciduous woodland tended to have deeper, shorter bills. Further, within a species such as the Coal tit or Great tit, individuals from coniferous woodland populations also tended to have longer, thinner bills than those from deciduous woodland. This difference was most strongly reflected in the bill index (bill depth/bill length) which was on average reduced in coniferous woodland. This pattern of variation was found widely across Europe. Snow (1953) and Partridge and Pring-Mill (1977) found that Blue tits feeding in pines in the Canary islands, had significantly longer, thinner bills than those in deciduous woodland. Grant (1979) suggested that on 'pine islands' in the western Canaries the species had been forced to specialise in pine habitat. This had not occurred on more diverse islands in the eastern Canaries where the birds posessed an unspecialised bill.

Snow suggested that a thin bill was in some way adaptive in coniferous woodland. He suggested that possibly it was better for picking small insects from between the needles. Partridge (1974) pointed out that a fine bill is probably better for fine manipulation of small prey items since the bird would be able to see more of the bill tip. She likened this to using fine forceps. Similarly, a longer bill might bring the tip outside the minimum focussing distance of the bird's eye, again allowing greater control. Ulfstrand *et al.* (1981) have proposed a non-adaptive explanation for the widely observed relationship between woodland habitat and bill morphology and I shall discuss this critically in the next section.

In addition to differences in bill index between coniferous and broad-leaved habitats, a second broad trend in bill index exists in *Parus* species. Species such as the Great and Blue tits which take a larger proportion of seed in the diet (especially in winter) have a greater bill index than those such as

the Coal and Crested tits which take mostly insect food (when occurring syntopically). This broad pattern is comparable with the general difference in bill index between granivorous and insectivorous passerines (see chapter 4). Since seed food is available mostly on the ground whilst insect food may be found throughout the woodland profile, ground feeding tit species tend to have relatively deeper bills than those feeding higher. Hence in general terms, bill index and mean feeding height are negatively correlated among species (Snow 1953, 1954; Hartley 1953; Betts 1955).

The response of bill morphology to changes in niche will depend partly on the relative importance of selection for bill characters at different times of the year (Hespenheide 1971, Grant 1985) and partly on the nature of the niche shift involved. In the type (2) shift (selective shift) caused by interspecific competition, a shift in the mean of a relevant trophic character may occur with no change in the variance. This would correspond to a shift in niche location without a change in niche breadth. In allopatry, an increase in niche breadth would correspond to an increase in morphological variance in accordance with the variable niche hypothesis if intra-specific competition were intense enough to cause intraspecific niche segregation and associated morphological specialisation. In Parus, behaviourally dominant species tend also to be numerically dominant. Therefore intraspecific competition is likely to be less intense than interspecific competition for subdominant species because intraspecific aggression is partly a function of bird density relative to the abundance and distribution of food (Morse 1970, 1974, 1980).

Character displacement theory assumes that bill length, depth, or index correlates with the niche dimension along which a shift occurs. Most observed niche shifts in Parus occur in feeding station. If a species shifts feeding

height, but continues to feed in the same way, and upon the same type and size of food, no character shift should be expected. Hence some knowledge of the functional relationship between bill morphology and feeding ecology is required before correlations between niche and character shifts can be understood. Such relationships may vary between species since other aspects of their ecology will differ.

In the type (1) niche shift (behavioural shift), subdominants may show a shift in morphological mean or variance though again the rules for the application of the variable niche hypothesis will apply. Dominant species such as the Great tit will overlap little in absolute bill size with other tit species since they differ so much in body size. However, since the Great tit is both behaviourally and numerically dominant it is most likely to show intraspecific niche segregation resulting from intraspecific competition and so to age and/or sex-specific morphological variation.

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1.3 Bill variation in *Parus major*.

This section gives a brief introduction to previous work on bill variation in the Great tit. Most previous studies of bill morphology in the Great tit were concerned with the species role as part of a community, rather than with intraspecific variation.

Prazak (1894) recognised the British Great tit as a distinct race *P. m. newtoni* largely on differences in plumage characters which are no longer recognised (see Appendix 4). Hartert (1907) and Witherby (1938-41) pointed out that the British race could be distinguished from that of the European continent on the size and shape of the bill, and that this was probably the only consistent difference. They stated that the bill of the British birds was deeper and showed a straighter culmen than the continental *P. m. major*, but they also noted that the distinction was subjective and ideally required simultaneous examination of specimens of both races to make a diagnosis. Harrison (1945) examined 50 skins of *newtoni* and 50 *major*. He found that 42% of *newtoni* had a straight culmen (judged by eye) whilst only 4% of *major* skins had (96% had a decurved or convex culmen). He also found a tendency for *newtoni* to have a greater bill coefficient (depth x breadth) than *major*. I have tested Harrison's data by t-test and find this 'tendency' to be highly significant ($t_{(98)}=10.725$, $P<0.001$). However, Harrison considered that the southern English populations were not genetically isolated from the continent so that the situation might be rather 'fluid' between the nearest populations of the two races.

The major contribution to the analysis of bill variation in the Great tit was made by Snow (1953, 1954). His findings are summarised below:

(1) Body size (as defined by wing length) in newtoni conformed to a cline related to mean annual temperature. That is, across Europe (including Britain) body size varied in accordance with Bergman's rule. Two populations, one from North Africa, the other from southern Persia (now Iran), did not conform to this trend.

(2) Among populations, bill length was positively correlated with winter temperature above 27°C in agreement with Allen's rule. There was no correlation below this temperature. This may reflect either an anatomical or an ecological constraint on the minimum bill length.

(3) Bill length and wing length were positively correlated among populations, but due to opposing selection for the two traits following Bergman's and Allen's rules, the correlation was weak (r_{32}=0.39, P<0.05).

(4) Bill depth among sixteen populations across Europe was significantly and positively correlated with wing length, but two British populations showed rather greater bill depths than expected for their means of wing length. The bill depth deviation from the clinal trend for P. m. major, was in the direction claimed by Harrison (1945).

(5) Males averaged significantly larger than females in all body characters (wing, tarsus, tail).

(6) There was no significant sexual dimorphism in any bill character. Bill length was 0.1 mm longer (averaged across populations) in males than in females. Snow argued that the similarity of bill measurements between sexes despite the great differences in other characters was evidence for the importance of absolute (rather than relative) bill size in the Great tit.

(7) Finally, (as already described), he found that the bill index of birds from coniferous woodland areas was consistently less than that from broad-leaved areas. This trend was not tested statistically.

Snow's work forms the background for all future work on bill morphology in the Great tit, and places great emphasis on the assumption that bill variation is adaptive.

Ulfstrand et al. (1981) examined bill variation among 'conifer' and 'broad-leaved' woodland populations of the Great tit in Sweden during the breeding season. They found that bills were thinner on average in coniferous woodland, as predicted by Snow. However, they proposed a non-adaptive explanation for this pattern of variation. They suggested that first-year birds might be more likely to breed in sub-optimal habitat. Van Balen (1973) showed that conifer woodland was sub-optimal to broad-leaved for the Great tit. Krebs (1971) found that first-year birds were more likely to be excluded from optimal habitat when space was limiting. Also these birds were more willing to vacate territories in such habitat when space became available in optimal habitat. Hence Ulfstrand et al. suggested that a net movement of birds might occur from coniferous woodland to broad-leaved woodland as the birds became older. If bill size correlated with body size (body size increases with age, Van Balen 1967) or was itself age-dependent, the observed differences in bill size between habitats could result from age-dependent movement alone. However, they were unable to show a significant correlation between bill size and body size. Nor could they find evidence for age-specific variation in the bill. And indeed, although they found slightly more first-year birds breeding in coniferous woodland than in broad-leaved, this difference was not significant. Hence (despite the emphatic presentation) their results were far from supportive of their hypothesis. However, their suggestion that the habitat-specific distribution of bill variation might have a non-adaptive source, ultimately related to intraspecific dominance, is important.

Van Balen (1967, 1973) and Bjorn (1960) found that the degree of sexual

dimorphism in characters related to body size varied between populations. In particular, populations were more dimorphic in broad-leaved woodland than in coniferous woodland. In addition, the degree to which plumage and body size varied with age also differed between populations. If sex and age differences were indicators of intraspecific competition, they argued that this was more intense in broad-leaved woodland where the density of birds was higher. The reduced sexual dimorphism in coniferous woodland was due to a reduction in the mean size of males in that habitat. This may reflect reduced inter-male rivalry leading to reduced sexual selection in the lower density population. Alternatively it might reflect an environmental constraint on body size caused by the lower abundance of food. If bill size is adaptive, bill characters should be selected for independently of body size (within the genetic constraints of pleiotropy, linkage and epistasis), so that there should be no a priori expectation of a correlation between bill and body-size.

Van Noordwijk and Klerks (1982) have looked at the heritability of bill characters in the Great tit population on the Dutch island of Vlieland. They found that 'narrow-sense' heritability estimates varied from 49% for bill-length to 68% and 71% for bill-depth and breadth respectively. The 20% difference between the estimates for the different characters implies a different environmental component of phenotypic variation in the three characters. Hence the three characters may be differentially selected or show different repeatability, although correlations among the characters may obscure the results of selection (Grant 1985). Van Noordwijk and Klerks (1982) also obtained higher estimates of heritability than repeatability. That is, birds were more like their parents than like some previous measurement of themselves! This suggests that heritability estimates might have been elevated by an environmental influence that was shared by both

parents and offspring. Also, since repeatability (variance among individuals / total variance) must set a ceiling for estimates of heritability (Falconer 1981), they suggested that seasonal variation may occur in the bill of the Great tit. Since bill characters are heritable, variation may also occur through natural selection (Endler 1986).

Van Noordwijk and Klerks (1982) also found that 6.35% of birds handled showed clear defects in the bill. These were generally observed as a badly overgrown upper mandible or as breaks in the tip or tomia. Such abnormalities have frequently been reported in the Great tit and in some cases (Howard 1951) may help to shed light on the processes involved in bill-size determination. This is discussed further in section 3.7.

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1.4 Aims and layout of the thesis.

The broad aims of this study are to determine the relationship between ecology and bill variation in the Great tit, and in particular, to fill many of the gaps in knowledge outlined in the introduction above. In so doing, I hope to shed light on the processes described by Lack (1971) and Grant (1972) relating competitive exclusion to character displacement. Similarly, I hope to test Van Valen's (1965) variable niche hypothesis and to determine the role played by intraspecific competition mediated by social dominance in determining morphological variation (Morse 1974).

Chapter 2 describes the study site and general methods employed, although further specific methods will be described in the relevant chapters. It also considers the problems of bias in sampling the tit population.

Chapter 3 describes the patterns of variation in bill characters in the Great tit study population with respect to sex, age, season and gene flow. It also considers the repeatability, heritability, growth and development and mode of change of bill characters within individuals.

Chapter 4 considers the relationship between the bill variation described in chapter 3 and ecology in winter. In particular it discusses bill variation between classes in relation to observed differences in niche. This leads to a discussion of the adaptiveness of bill characters in winter and a laboratory experiment designed to test the efficiency of prey handling by birds with different-sized bills. A method is described to assess the condition of individuals using a measure of fat reserves, and the relationship between this and bill size is discussed.

Chapter 5 continues the theme of bill variation in relation to ecology but

considers its importance in summer. A new method for analysing prey size in relation to bill size is described. Bill size is then related to individual fitness through its effect on breeding success.

Chapter 6 examines the relationship between bill size and breeding habitat. First a simple classification of habitat which is independent of the parameters under investigation is described. Two analyses of bill variation are then carried out within this habitat framework. The first considers the same phenotype in different environments. The second considers different phenotypes in the same environment.

Chapter 7 examines evidence for natural selection of and for bill characters within the study population during the course of the project. This is considered principally in terms of the 'conditions for selection' and fitness variables described by Endler (1986).

Chapter 8 attempts a synthesis of the results presented throughout the thesis in relation to the ecological hypotheses presented in the introduction. In particular, character displacement, morphology as a function of social dominance, and the variable niche hypothesis are considered as determinants of the observed patterns of variation.

The reader should also note that a short glossary of terms is included before Chapter 1, and Appendices 3 and 4 include a number of original analyses.

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Chapter 2. Study site and methods.

Chapter 2. Study sites and methods.

2.1 The study site.

The study was principally carried out between May 1982 and July 1985 (although some additional data were recorded during the winter of 1981/82), as part of the long-term population study of the Great tit of the Edward Grey Institute at Wytham woods.

Wytham woods (hereafter referred to as Wytham) comprise some 320 hectares (800 acres) of woodland lying about 4 km west of Oxford. Most of the vegetation is broad-leaved woodland although a considerable area has been planted with conifers since about 1930. The woodland area of the estate is divided into forestry compartments, each being more or less distinct in its management history and vegetation. The estate stands on Wytham hill which rises to 165 m. The hill presents a series of geological strata from a capping of Corallian limestone, through sands to clays at the foot (about 60 m above O.D). Hence aspect, altitude and geology all contribute to the variation among compartments although management history is perhaps the most important.

Much of the conifer plantation is of Larch Larix decidua and Norway Spruce Picea abies. These plantations vary greatly in age and therefore height. Most were interplanted as a 'nurse' crop with broad-leaved trees, usually of Oak Quercus robur so that there is little pure conifer woodland. Single conifers, usually Scots Pine Pinus sylvatica, also occur occasionally within broad-leaved compartments. Four principal types of broad-leaved woodland can be recognised at Wytham.

(1) The 'ancient semi-natural woodland' contained within the biological reserve areas. This is typified by the relatively high density, diversity and

equitability of tree and shrub species, the uneven age structure of the woodland, the lack of Sycamore Acer pseudoplatanus and presence of Maple Acer campestris as a dominant species. The shrub layer is diverse and dense. These areas were formerly managed as coppice-with-standards. Apart from occasional coppicing, these areas are undisturbed.

(2) Sycamore woodland introduced to Wytham largely in the 16th century (Elton 1966). This is typified by a relatively low density and equitability of tree and shrub species due to the dominance of large mature Sycamore. Some compartments of this habitat type also show a greatly reduced tree and shrub diversity. Maple occurs rarely in this woodland type and the herb layer is frequently dominated by Nettle Urtica dioica. The shrub layer is usually sparse or absent. Management currently involves periodic coppicing and/or thinning of standard trees.

(3) Young Broad-leaved plantation under 50 years of age and typified by the even-age structure of the woodland. Monocultures of Oak, Ash Fraxinus excelsior, Beech Fagus sylvatica, Sweet Chestnut Castanea sativa and mixed plantations including Hornbeam Carpinus betulus occur. The shrub layer may be diverse or absent, but is usually sparse and contains species found rarely in the other woodland types such as Holly Ilex aquifoliata.

(4) Mature Beech plantation over 150 years of age and dominated by Beech. These are the principal mast producing areas and vary in diversity from pure beech plantation (such as Brogden's belt) to a fairly equitable mixture with Oak, Ash, Sycamore and, less frequently, Lime Tilia sp. with a well developed shrub layer containing Hazel Corylus avellana coppice, and Hawthorn Crataegus spp. A habitat classification based on these principal woodland types is presented in chapter 6. Oak is present in varying densities in all these woodland types, in some areas representing a relict of older woodland.

Elton (1966) and Lack (1966) give good accounts of the vegetation of Wytham hill although these are somewhat out-dated due to changes in management practice. In particular, a number of Sycamore woodland areas have been extensively thinned since the start of the present study, and where relevant I shall refer to this later.

The long-term Great tit study was started in 1947 by David Lack. He erected a number of wooden nesting boxes in Marley Wood, Wytham to obtain basic breeding data (clutch size, laying date etc) following the methods of Kluijver in Holland who took over the first nest-box population study begun in 1912, by Wolda (kluijver 1951). In the late 1950s and early 1960s, the number and distribution of boxes were expanded to cover the whole woodland area of the estate. There are today over 900 nest boxes available to the birds. For logistic reasons the boxes are divided into study areas or 'rounds' roughly corresponding with the forest compartments. For management reasons few boxes have been placed in conifer areas. This, together with the interplanting of conifer with broad-leaved trees has made a comparison of bill morphology between conifer and broad-leaved woodland unpracticable in this study. However, the mean dispersal distance of Wytham Great tits is greater than the mean diametre of conifer stands available (Greenwood et al. 1979). Hence provision of nest sites in conifer areas is unlikely to produce a genetically determined relationship between bill and habitat (so defined) in this population. The tit population in the wooden nest boxes suffered heavy predation in some years from Weasels Mustela nivalis (Dunn 1977) and Great-spotted Woodpeckers Dendrocopas major (Perrins 1979 and refs cited there). Hence in the mid 1970s they were replaced by concrete German-made boxes suspended by a wire from a bracket on the tree. Predation is now a minor cause of brood-loss.

TABLE 2.1 Nest box areas used in the present study.

Round	Woodland[1]	Area[2]	comps[3].	Conif[4].	No.nestboxes	Altitude[5].
E	C,2,3,4,5	60.7	16	3	138	92-165m
CP	c,2,3	19.0	4	1	50	84-122m
W	1,5	25.9	4	0	105	61- 92m
total:		105.6	24	4	293	

Notes (1). Woodland habitat types. C - major stands of conifer, c - occasional single or a few conifers, 1 - ancient woodland, 2 - sycamore woodland, 3 - young broad-leaved plantation, 4 - beech woodland, 5 - scrub.

(2). Area is given in hectares (from Minot & Perrins 1986).

(3). The number of forest compartments.

(4). The number of compartments containing conifer plantation.

(5). Altitude range given in metres above Ordnance datum.

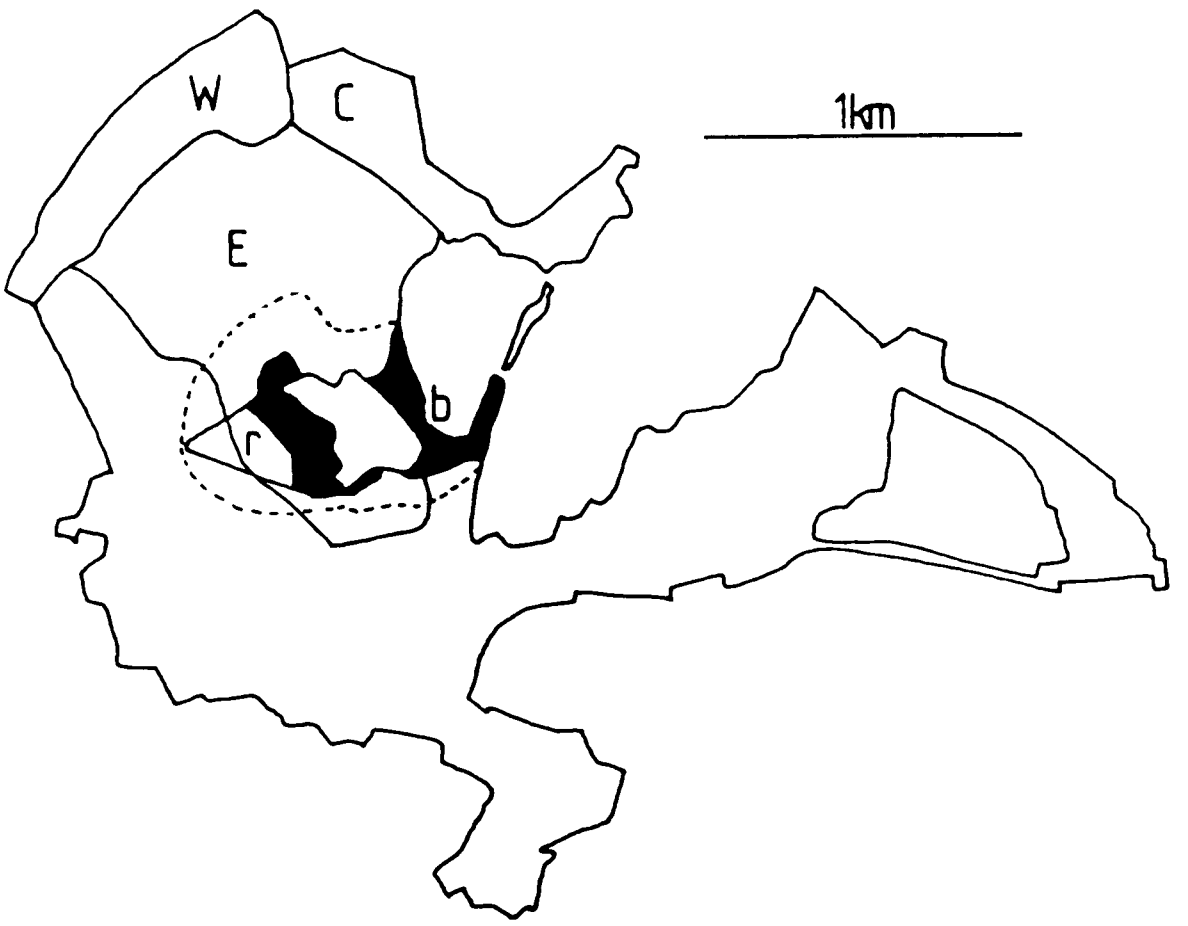


Figure 2.1. Wytham Woods study sites. Nest box areas: E-Extra, C-Common Piece, W-Great Wood. Block shading - main beechmast producing areas. r-Rough Common, b-Brogden's Belt. Dashed line - limit of main winter trapping area.

The present study was carried out in the nest box rounds known as Extra (E), Common Piece (CP) and Great Wood (W). These areas together contain some 300 nest boxes and present all the major woodland types described above. Figure 2.1 shows the study areas. Table 2.1 gives a brief description of the habitat types in each round.

Winter-trapping was conducted in the same areas to ensure the highest rate of individual re-trapping between seasons. Winter sampling was concentrated on the hill-top beech wood areas shown in Figure 2.1. Further details of the study site and background to the long-term tit population study were given by Lack (1966) and Perrins (1963, 1965, 1979), and a comprehensive review of previous research and results of the study was provided by Perrins (1979).

2.2 Beech mast sampling.

The abundance of tree seeds as food in winter, and particularly of masting crops such as beech, is strongly correlated with over-winter survival of Great tits at Wytham. This may be true of adults (Clobert et al. in prep.) but is especially true of first-winter birds (Perrins 1965, 1966, 1979), although the relationship may not be a simple one (Perrins and Dhondt, in prep.). As a result, aggregations of up to 200 individuals may be observed, usually in early winter, feeding on beech mast in a year when the crop is good. The beech crop varies dramatically between years, trees and areas; and regular fluctuations (cycles) of crop quality have long been suspected in some areas (Watt 1923). Beech mast is taken by tits, finches (notably Fringilla spp.), nuthatches Sitta europea, Pheasants Phasianus colchicus, Wood Pigeons Columba palumbus, Great-spotted Woodpeckers Dendrocopos major, Grey Squirrels Sciurus carolinensis and several small mammals (Watt 1923, and own observation). Hence the predation rate for mast may reach 100% by the end of the winter in some years (Watt 1923). Mast feeding represents a major part of the seasonal shift in diet of the Great tit. Hence some estimate of the relative quality and distribution of beech mast in the study area was required.

Most of the beech crop has fallen by the end of November. Figure 2.2 shows the distribution of beech trees in the winter trapping area drawn from aerial photographs. The overall sampling area was divided into fifteen mast sub-sampling areas (Fig. 2.4). In each winter an estimate was made of the amount of seed produced in each area. The seed crop was first assessed qualitatively as good, moderate or poor. Then, during the winter of 1983/84 30 marked $1m^2$ quadrats in each of three sampling areas (designated A1 - A3) making 90

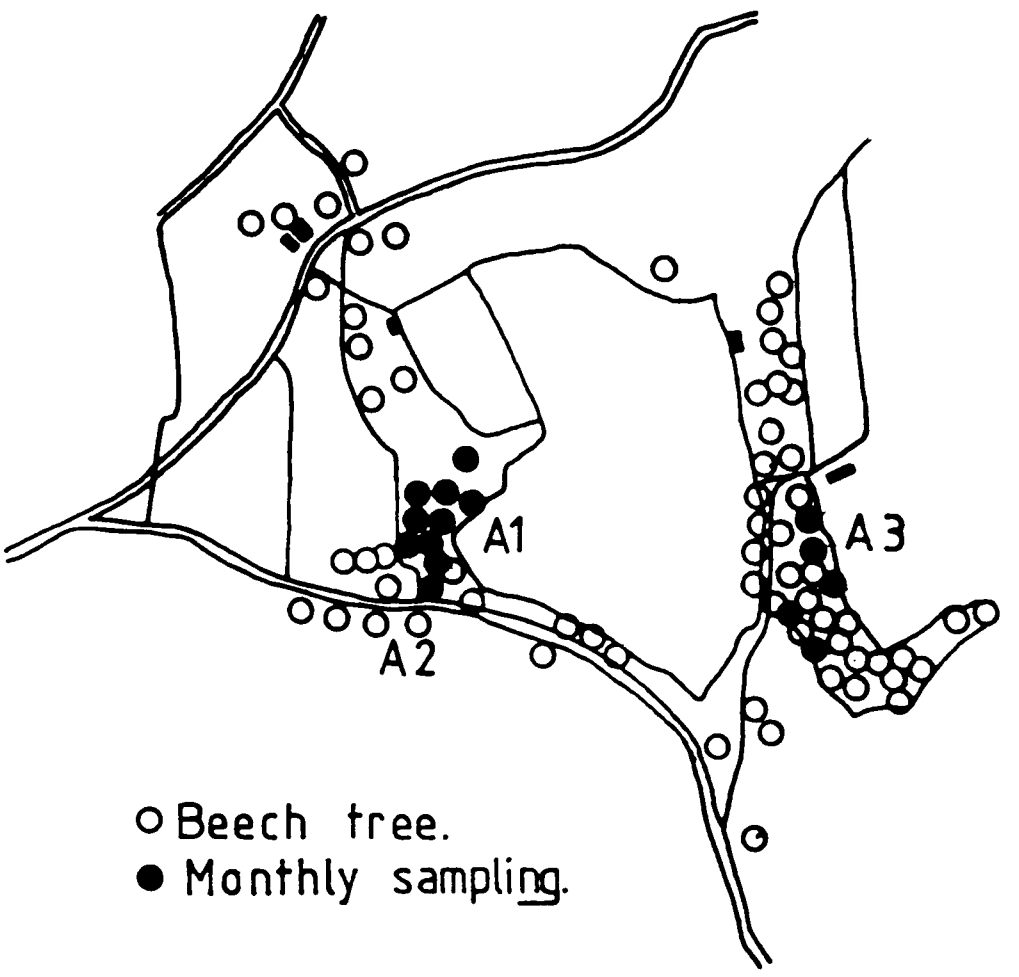


Figure 2.2 Beech distribution in the winter trapping area on Wytham hill. Monthly sampling areas labelled A1 - A3.

quadrats in all were sampled at 30 day intervals from October to March inclusive. Six quadrats were sited beneath each of five trees in each sampling area (5 and 10 m from the bole), making 15 trees in all. Each month the number of new seeds in each quadrat was recorded. The seeds were then removed so that an estimate of the total seed input during the previous month could be obtained. This gives an underestimate of the true input since it excludes seed already taken by predators. However, after the first sampling, quadrats contained less seed than the surrounding area so that predators should at least show no preference for feeding in the quadrat area. Figure 2.3 shows the monthly seed input and cumulative total seed input for each of the three areas. From these estimates, the qualitatitve crop estimates for the fifteen sampling sites could be roughly defined in terms of actual seed densities up till the end of November as follows:

Good >201 seeds m^{-2}.

Moderate 51-200 seeds m^{-2}.

Poor <50 seeds m^{-2}.

Figure 2.4 shows the beech crop quality in each of the fifteen sampling areas in each winter. Note the apparent alternation in seed abundance between areas in different years. A second qualitative estimate of seed availability in the three main sampling areas was made at the beginning of February each year. The relationship between the beech crop and Great tit sampling is discussed in the next section. Its relationship to feeding ecology is considered further in chapters 4 and 9.

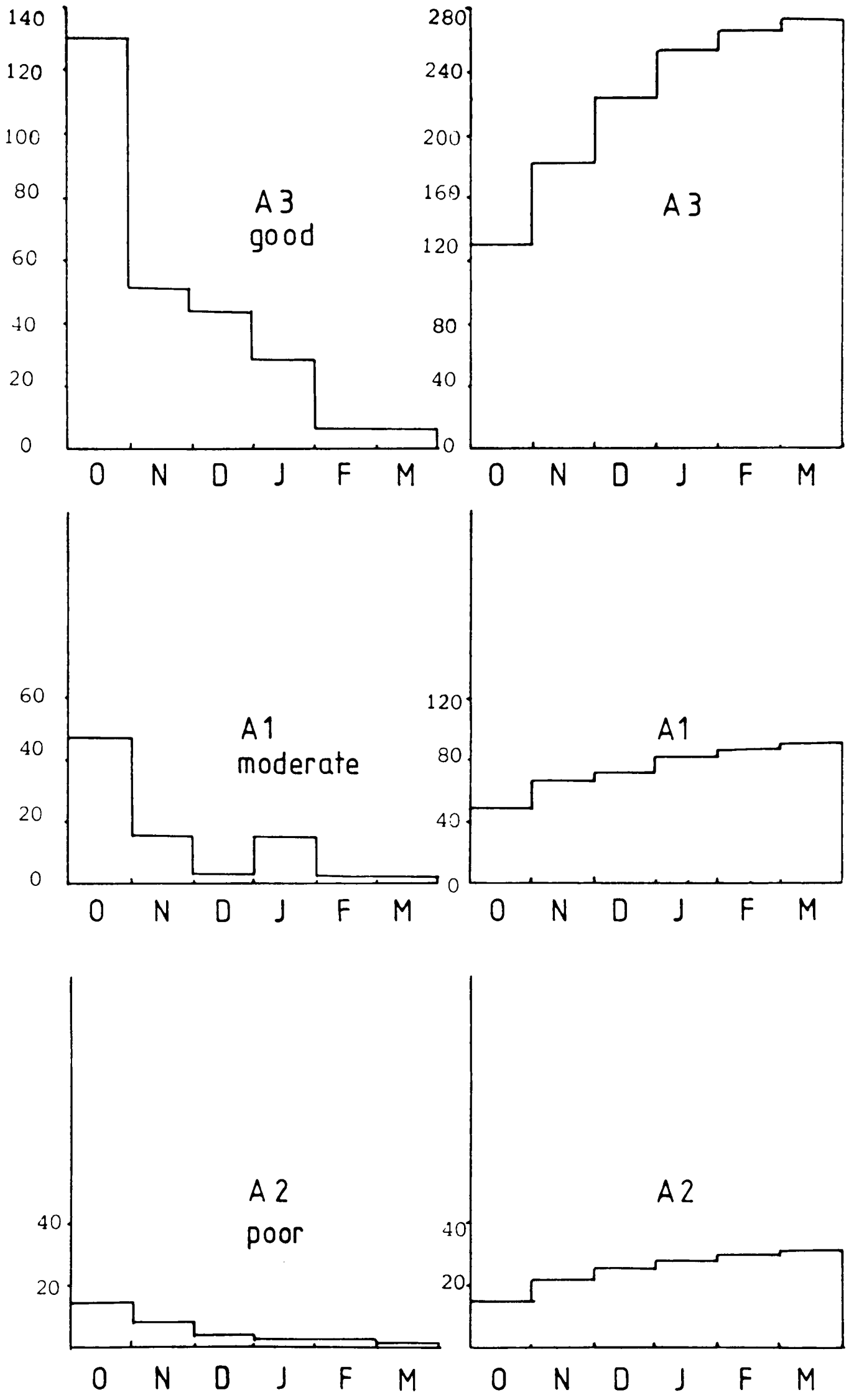


Figure 2.3. Monthly totals of Beech seed falling during the winter of 1983/84 in each of the three sampling areas shown in Figure 2.2 and described in the text. Totals are expressed as seeds m^{-2} averaged across thirty 1m quadrats in each area. The histogram on the left in each case shows the monthly seed input. This is expressed as a cumulative total in the right-hand figure.

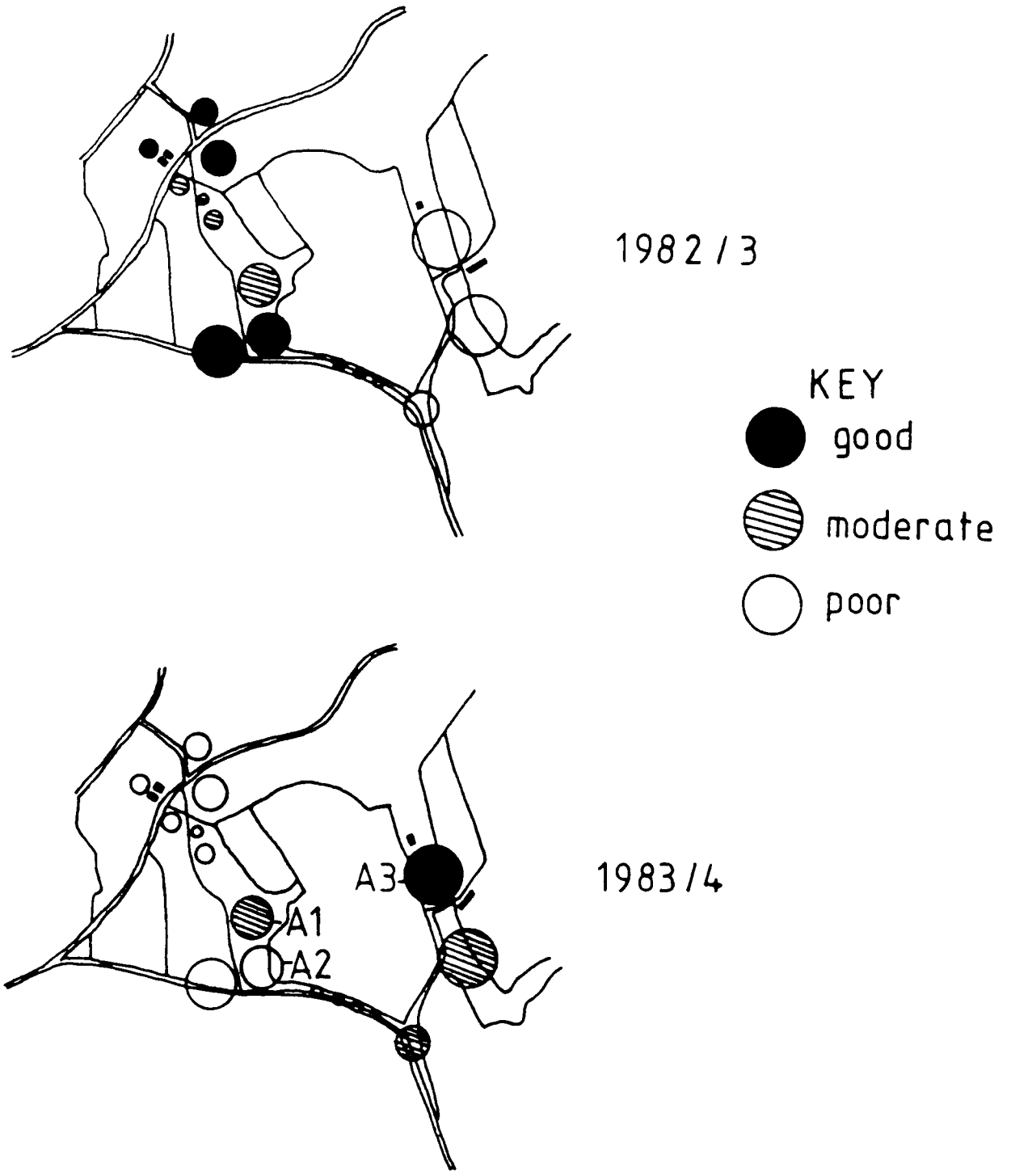


Figure 2.4. Beech crop quality in each of fifteen sampling areas in each winter. The qualitative assessment was based on the quantitative study (results shown in Figure 2.3) carried out in areas A1-A3 described in the text.

2.3 Sampling the Great tit population.

The Great tit population may be readily sampled in both summer and winter but sampling is subject to different biases in each season. Like other Parus species, the Great tit nests in holes and is easily attracted to artificial nest boxes. Perrins (1979) estimated that usually 100% of breeding pairs at Wytham occupied such sites. (Clobert et al. in prep. estimate by other means that not less than 95% breed in boxes), hence near total sampling of the breeding population is theoretically possible (subject to catch rate). In winter they may be trapped by mist net whilst feeding on beech mast, or when this is not possible, they may be attracted to peanuts or fat (Buxton 1948) provided as bait. However, although unbiassed sampling of the breeding population may be possible, it is difficult to assess the possible biases inherent in winter sampling. This is considered below.

The methods for sampling the breeding population were outlined by Perrins (1979). The eggs are laid during the latter half of April and first half of May. Clutch size varies up to a maximum of fourteen with a mean of nine. One egg is laid each day until the clutch is complete whereupon incubation commences. Incubation may start before the last egg has been laid in late clutches. Incubation by the female lasts for about fourteen days. The parents were trapped in the box using a trap-door trap triggered by the bird entering. This was done only after the chicks had reached six days of age as there is a risk of parental desertion before this age. The trapping success for females was close to 100%, that for males slightly lower due to their greater wariness at the nest. The chicks grow rapidly and reach plateau weight by their fourteenth day (day one is hatching day). On the fifteenth day the chicks were

individually ringed and weighed. The young fledge at between 18 and 21 days. All nestlings in boxes were ringed and weighed. These are the basic details of the breeding biology although deviations from this pattern are not rare. Clutch size varies between females and with date. Laying date also varies among females and with spring temperature, and incubation period may vary slightly. Table 2.2 shows the number of pairs breeding in boxes in Extra, Common Piece and Great Wood during the four breeding seasons 1982-1985 together with essential details of trapping and breeding success. That is, the total sample available for study.

For analytical purposes, the study period has been divided into three seasons as follows: (1) summer constitutes the breeding season. For trapping purposes this is May and June. In summer each adult was handled once only to reduce the risk to the young. (2) Autumn is defined as October to December. (3) Spring is defined as January to March. McCleery and Perrins (1985) found that a similar division of the winter seasons (though not the same) was useful in the analysis of survival. A marked decline was found in the availability of beech mast between Autumn and Spring (see Figure 2.3). Elton (1966) reported a similar decline in the abundance of invertebrates through the winter in Oak woodland. Hence the present division of the winter months allows an analysis of morphology under different levels of food availability.

All winter trapping was carried out by mist net as described by Perrins (1963). Although mist netting has many advantages over other methods of sampling (especially in allowing capture without bait, and increased sample sizes), it is not free from bias. However, most capture bias is a function of the baiting regime rather than the traps themselves. Where bait is provided predictably in time, dominance hierarchies may be established at a feeder so that trapping shows a strong bias in favour of dominant birds and in

TABLE 2.2 Essential breeding data for Extra, Common Piece and Great Wood for 1982-1985. N = Nº. note: 1 = number of nests at which young were ringed.

YEAR	estimated N pairs	N nests ringed[1]	N Young ringed	N females trapped	N males trapped
1982	83	73	616	79	71
1983	143	133	1156	126	112
1984	98	84	618	91	82
1985	69	6Ø	514	65	63

particular, adult male territory holders (Drent 1983). Bias related to bait regime may be avoided by trapping whenever possible in beech areas when the birds were feeding on beech mast, although at these sites there may be a bias against dominant classes (see analysis below). Trapping in Beech areas was achieved for periods in each winter. When mast was not available, bait was provided for short periods and randomly in time to avoid habituation to a food source. The effect of dominance on trapping is reflected in the retrap rate for birds of a class at baited and unbaited sites. Figure 2.5 shows the percentage of birds of each class trapped once, twice etc at baited and unbaited sites. Only Wytham hatched birds (hereafter referred to as residents) were used in this analysis to ensure that all birds had been in the population for the same period of time (ie: all equally "at risk"). Data have been pooled among seasons for this analysis. Mann-Whitney U tests were carried out on each of these pairs of distributions (that is 'baited' versus 'unbaited'). Only the comparison for adult males was significant ($W=125$, $P<0.05$). Overall, the retrap rate was very low as shown by Figures 2.6 and 2.7 which show frequency histograms for male and female retrap rates respectively. These figures are for all birds handled, and not residents only.

Table 2.3 further subdivides winter trapping samples to test for an age bias between baited and un-baited sites within seasons and sexes. This suggests that there is a tendency to catch more first-year than adult males at unbaited sites, and more adults than first-years at baited sites. This result is influenced by the tendency to retrap adult males more at baited sites. However the very low number of adults trapped at unbaited sites demonstrates that it is a real effect. There was no such bias in female trapping. Sampling bias of this sort does not necessarily influence the results of analyses of

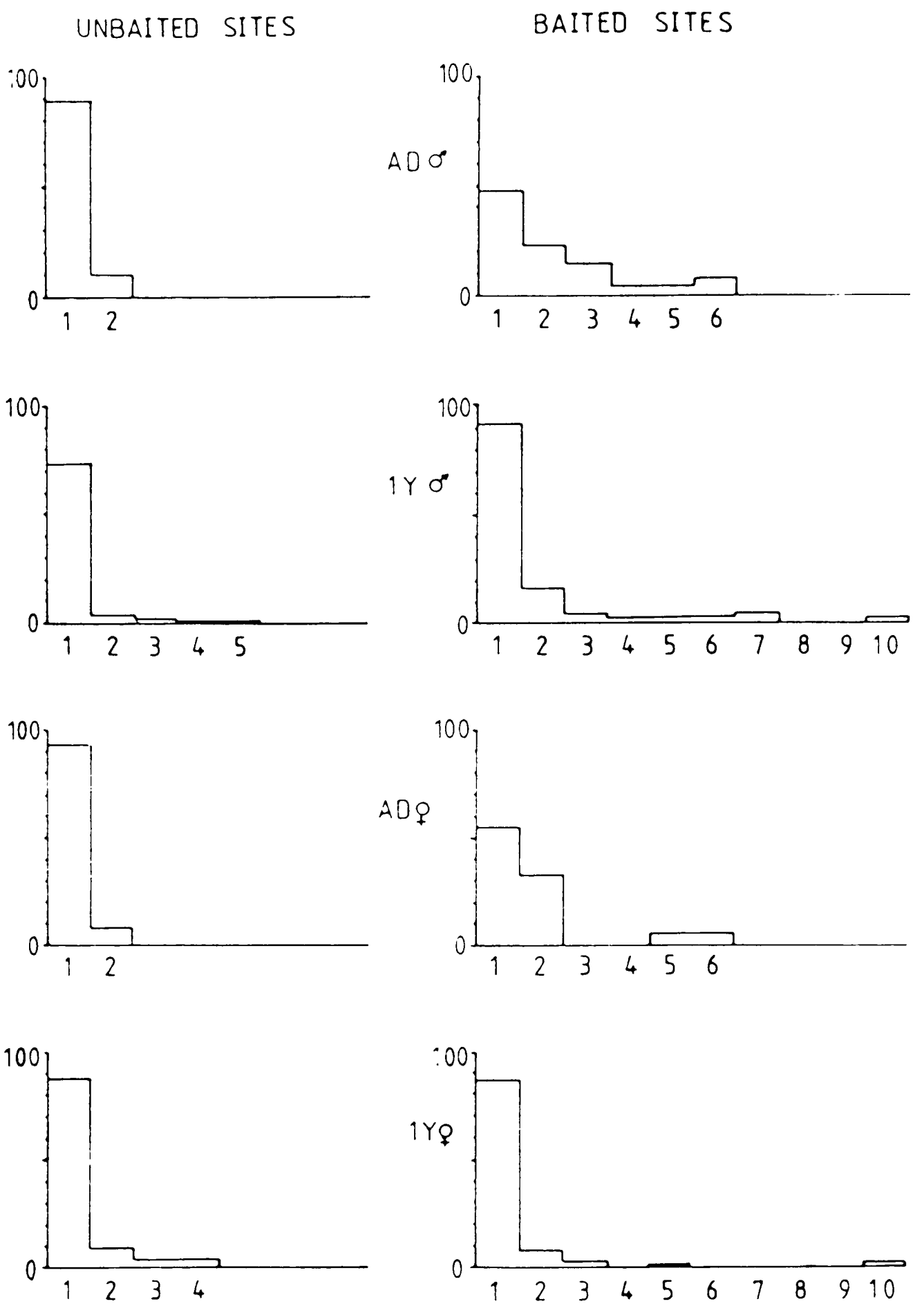


Figure 2.5. Relative frequency histograms showing the retrap rates of Great tits in each age/sex class at baited and unbaited sites. Data from all winter captures of resident (Wytham-hatched) birds were used to construct the figures. Adult males showed a significantly higher retrap rate at baited sites than at unbaited sites. No other comparisons gave significant results - see text for details.

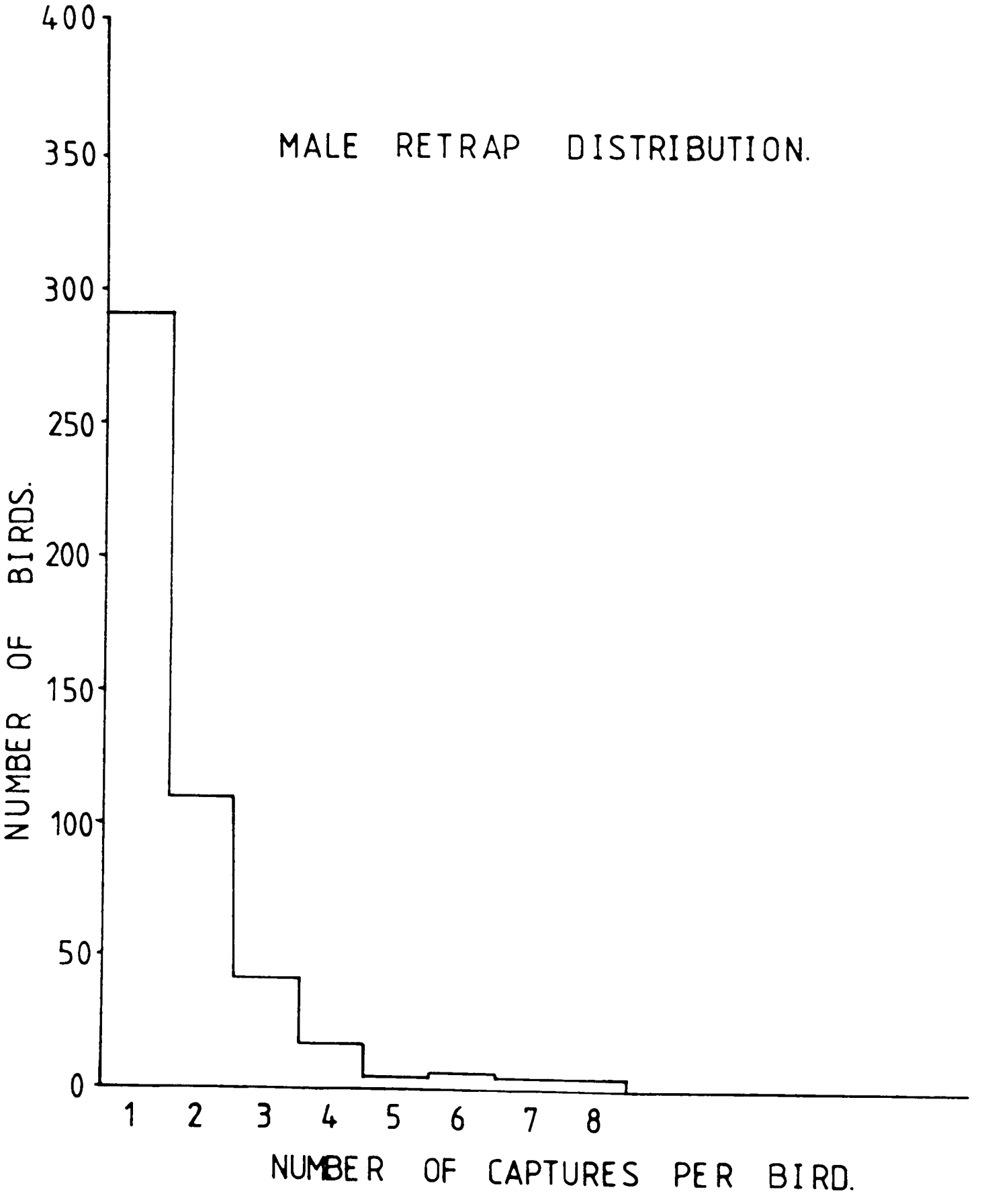


Figure 2.6. Frequency histogram showing the distribution of captures of all male Great tits during the study. This includes recaptures made within and between seasons, and in both summer and winter. Most individuals were handled once only, and very few were retrapped more than three times.

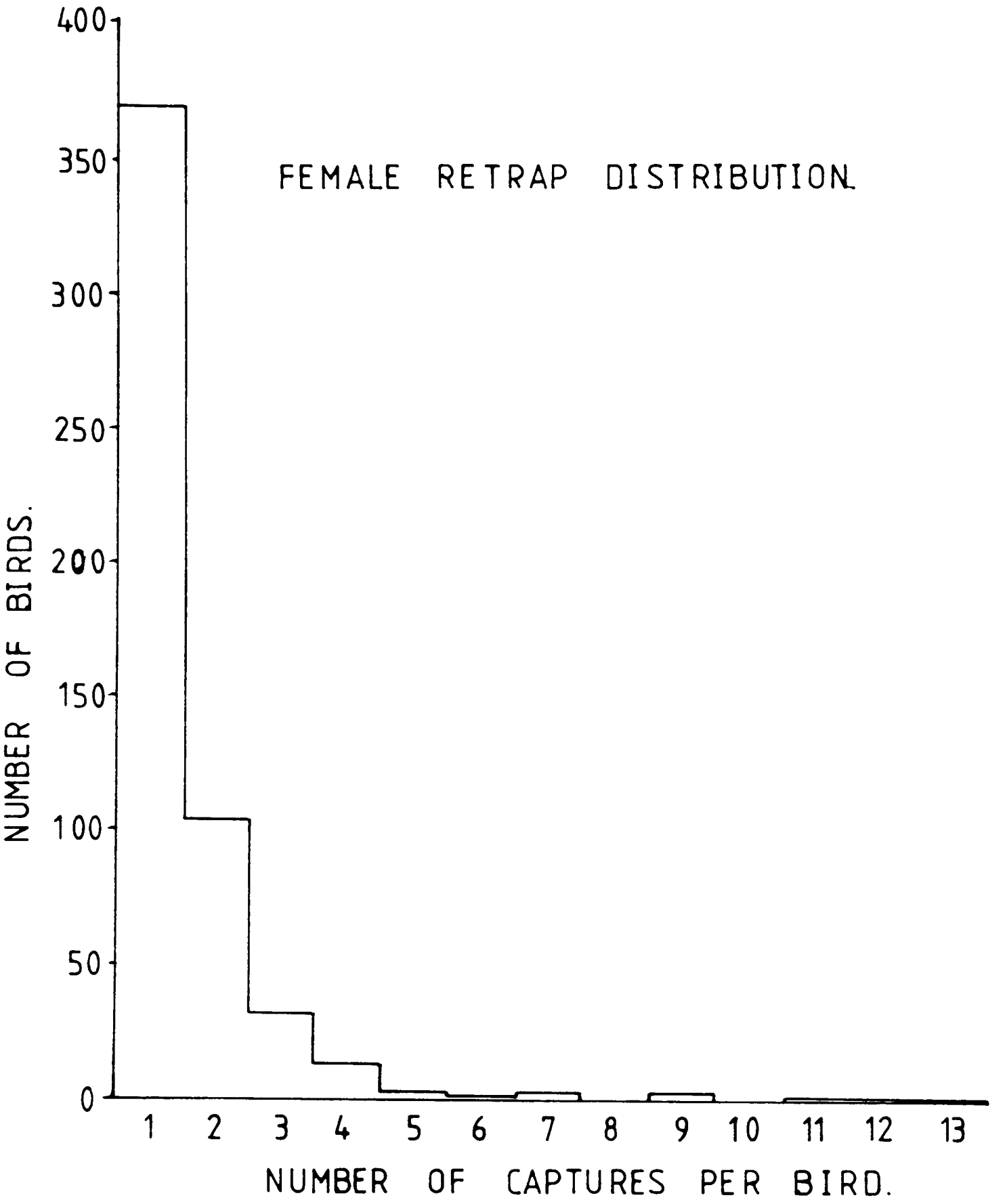


Figure 2.7. Frequency histogram showing the distribution of captures of all female Great tits during the study. This includes recaptures made within and between seasons, and in both summer and winter. Most individuals were handled once only, and very few were retrapped more than three times. The maximum capture rate (13) was greater than that for any male (8) - see Figure 2.6.

TABLE 2.3 Number of handlings of resident first-year and adult, males and females trapped at baited and un-baited sites in each season, together with a Chi-square test for association (df=1).

MALES

SEASON	Age	Baited	Unbaited	Chisquare
Aut 82	1Y	38	Ø	-
	Ad	1	Ø	
Spr 83	1Y	47	1	-
	Ad	26	Ø	
Aut 83	1Y	26	47	8.1Ø **
	Ad	5	Ø	
Spr 84	1Y	5	6	3.88 *
	Ad	16	4	
Aut 84	1Y	46	45	Ø.92 NS
	Ad	3	1	
Spr 85	1Y	3	17	6.56 *
	Ad	7	5	

FEMALES

SEASON	Age	Baited	Unbaited	Chisquare
Aut 82	1Y	28	Ø	-
	Ad	1	Ø	
Spr 83	1Y	24	1	-
	Ad	8	Ø	
Aut 83	1Y	8	29	3.ØØ NS
	Ad	2	1	
Spr 84	1Y	7	Ø	1.51 NS
	Ad	13	3	
Aut 84	1Y	37	29	Ø.43 NS
	Ad	4	5	
Spr 85	1Y	1	3	Ø.35 NS
	Ad	3	4	

morphological data. However, I shall show in Appendix 3 that the weight of birds may be influenced by the predictability of the food supply in winter. This is especially true for adult males. I shall also show that when food is provided unpredictably in time as was done throughout the present study, there is no significant effect of baiting on body weight. Bias in sampling bill characters may arise if individuals are distributed between sampling areas according to differences in morphology, as might occur due to differences in habitat selection, and if birds in different habitats have different probability of capture. Where possible, I shall make use of tests to determine the possible effects of sampling bias on the pattern of morphological variation described.

A likely cause of the significant association between age and bait in males demonstrated in Table 2.3, is that provisioning encourages male territory holders to remain on their territories through the winter. Figure 2.8 shows the distribution of 1983 nest sites from which birds travelled to feed at three trap sites during the winter of 1983/84. The Rough Common feeder (r) and Upper Seeds Common feeder (u) were baited unpredictably in time. At the third site - Brogden's Belt (b), birds were netted whilst foraging for mast in a pure stand of mature beech. There was no significant difference in the median dates of trapping at the three sites. The mean distance travelled by adult male territory holders to the feeders was 0.14 $\pm$ 0.07 km. The mean distance travelled to Brogden's Belt was 0.55 $\pm$ 0.18 km. This difference was highly significant (t_{16}=6.068, P=0.001). Only a single male from the Rough Common and Upper Seeds territories was caught in Brogden's Belt and that bird returned to breed in the same nest box in 1984 (sample sizes for these analyses are indicated in Fig. 2.8). The mean distance between Brogden's Belt and the territories from which Rough Common and Upper Seeds Common birds had come was

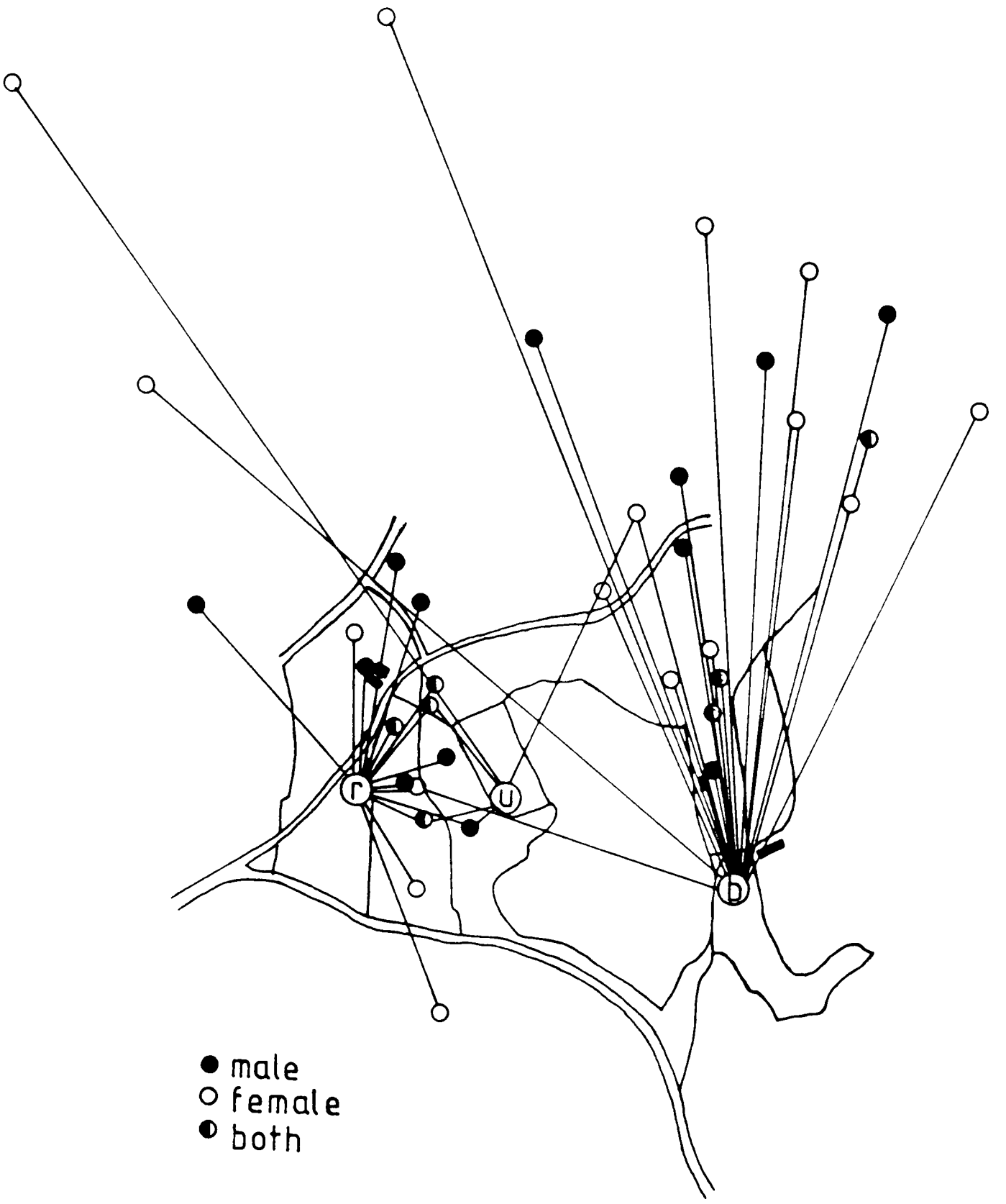


Figure 2.8. The distribution of 1983 nest sites (territories) from which adults travelled to feed at three trapping stations during the winter of 1983/84. Food was provided at sites r and u and this reduced the probability of breeders in the immediate vicinity travelling to feed on beech mast at site b. See text for further discussion and analysis.

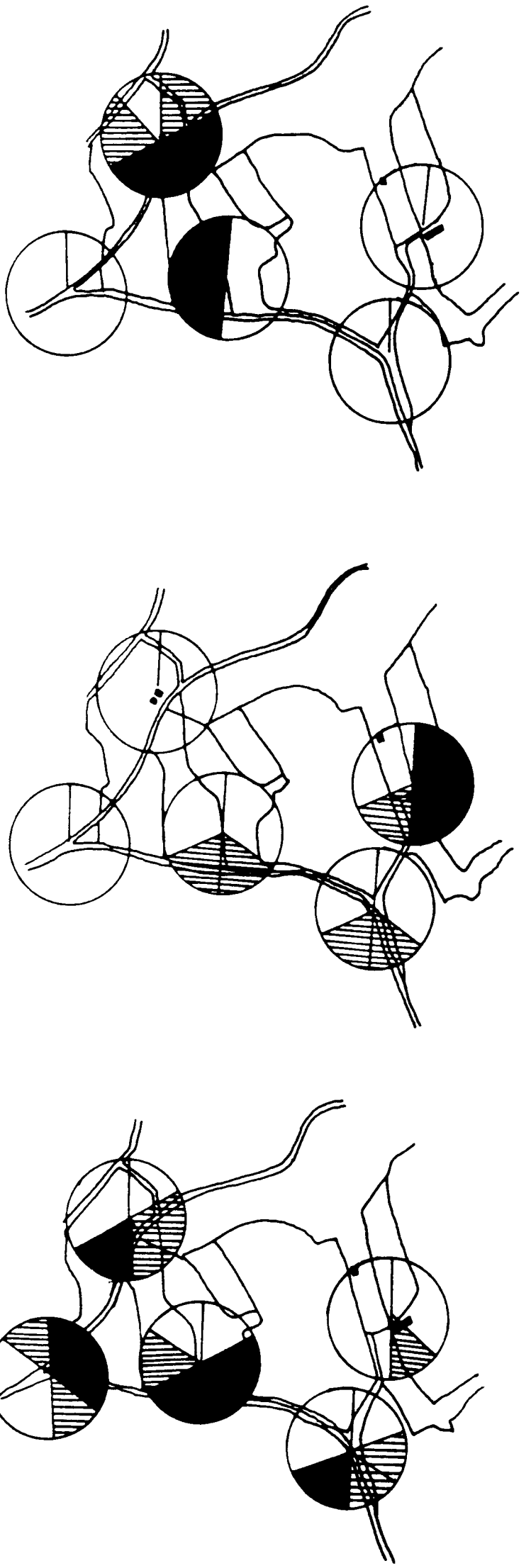


Figure 2.9. The distribution of Great tits during each winter month in the winter trapping area estimated from counts made during regular walks around the area. This should be compared with the distribution of beechmast shown in Figure 2.4.

only 0.3 km. This effective local isolation is important in a study of bill morphology in relation to local differences in food availability (chapters 4 and 9).

The number of Great tits observed feeding simultaneously in each of four main flock areas was estimated during walks around the study site each month during winter. The results are summarised in Figure 2.9 which shows the distribution of birds in the study area in each winter month. The maximum densities of birds recorded simultaneously on any single day are shown simply as 0, 1-50, and more than 51. A fifth site known as the Elder Patch (ep) (formerly the Five Sisters) attracted large numbers of tits to feed on a particularly heavy Elder Sambucus nigra crop in October and November 1984. Figure 2.9 should be compared with the distribution of beech mast in Figure 2.4.

Appendix 1 gives a summary of trapping totals for males and females caught at each site in each month of the study. A total of 1007 full-grown individuals were trapped and measured during the study. On average each bird was measured 1.67 times (see Figures 2.6 and 2.7). Throughout this thesis I use the terminology defined by the British Ringing Committee (Spencer 1975, 1984). A bird caught on a second or subsequent occasion is said to be 'retrapped' and is termed a 'retrap'. A bird found outside Wytham whether alive or dead is termed a recovery (the bird or ring having been recovered). A live recovery made by another ringer is a 'control' (the bird having been controlled). In addition, previous work on the Wytham population has differentiated between 'residents' - birds known to have hatched in the population, and 'immigrants' whose origins are unknown. A small proportion of immigrants were undoubtedly hatched in natural cavities in Wytham (Perrins 1979). On average, about 50% of birds breeding in any year are immigrants in origin (Bulmer and Perrins 1973).

2.4.1 Measurement of birds - Field methods.

On capture each bird was ringed (if not already), aged and sexed according to the criteria described by Perrins (1963, 1979) and Svensson (1975, 1984). Wing length was taken to 0.5mm on a stopped rule using the 'maximum chord' method (Svensson 1975). Garnett (1976) showed that tarsus length was the best predictor of body size that could be determined in the field in the Great tit. Tarsus length was taken to 0.5 mm using a stopped rule. This measurement was quicker to take in the field than the standard measurement taken to 0.1 mm with a vernier caliper from the nucal notch to the last complete podothecum (Svensson 1975). Figure 2.10 shows the relationship between these two dimensions. Although there is some loss of precision using this method (measurement is to 0.5 rather than 0.1 mm), there is no loss of accuracy (sensu Sokal and Rholf 1981). The calibration is highly significant, and allows comparison between the present measurements and previous data collected using the standard method (eg: Garnett 1976, 1981). Body-weight was taken to 0.1 g using a 50 x 0.1 g 'Pesola' balance and the time of weighing was recorded as the last full hour (GMT) passed. The amount of fat deposited within the furculum of the clavicle (claviculo-coracoid fat body, lieing within the furcular pit, or 'pit' below) was recorded as follows:

Fat Score	Definition.
0	No visible fat.
1	A little fat on the base of the pit
2	Base of pit obscured by fat, but less than half full.
3	Pit at least half full but below level of furculae.
4	Fat filling pit but not bulging above furculae.
5	Fat bulging above and overlying pectoral muscle.

This scoring is based on those described by Mcabe (1943), Czaja-Topinska

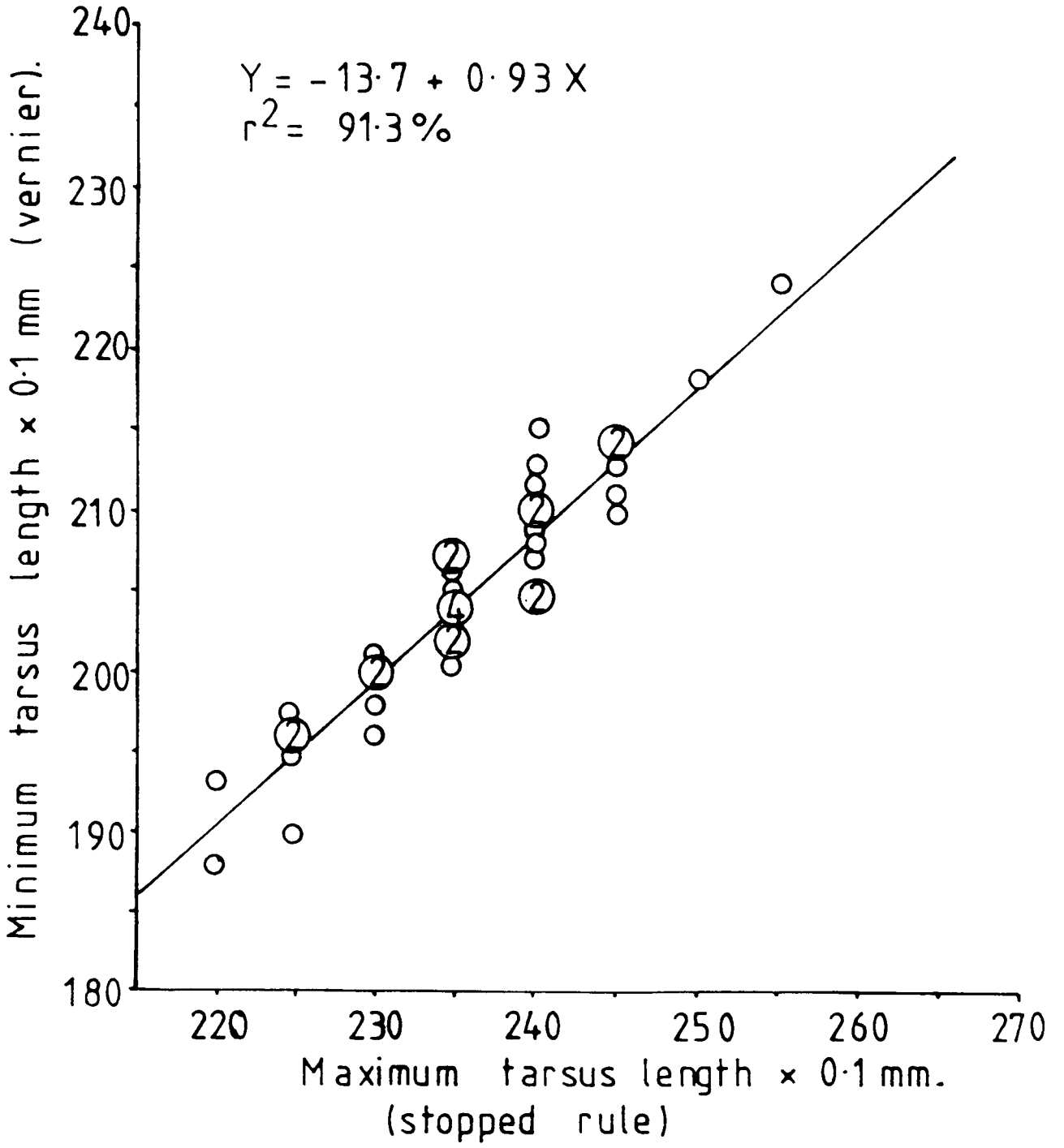


Figure 2.10. The calibration of tarsus measurement taken using a vernier caliper (measured to 0.1mm) with that taken using a stopped rule (measured to 0.5mm). The latter is more convenient to take in the field but is less precise.

(1969) and Spencer (1985).

A diagram showing the bill characters measured is given with the glossary. Bill length (culmen length) was taken to 0.1 mm from the base (naso-frontal hinge) to the tip of the upper mandible. Bill depth was measured to 0.1 mm at the deepest point of the gonys, anterior to the nares on the closed bill. Due to the retraction of the upper mandible allowed by rhyncho-kinesis of the bill, care was taken to ensure that the bill muscles were relaxed before bill depth was taken. Bill measurements were taken (and recorded) twice on each handling with a vernier caliper, and repeated if a difference of more than 0.2 mm was found, the average of these measurements was then recorded. All measurements were taken by the author. The ratio bill depth/bill length is the bill index (Snow 1953, 1954). It may be used as a third character giving some measure of bill shape though with reservation since differences in bill index may be brought about by differences in either of the constituent characters.

The accuracy of measurement for a character may be determined from the subsequent measurement of retraps, where re-measurement occurs within a sufficiently short duration that growth and/or wear should not have altered the true dimension. The 'short-term' repeatability of the character therefore expresses the inverse of observer error (ie: observer error = 1 - repeatability). It may be derived as the ratio of between-bird mean square/ total mean square in a one-way ANOVA (Falconer 1981). Table 2.4 gives short-term and long-term (ie: across all seasons within birds) repeatabilities for all characters. Short-term repeatability was calculated for 113 individuals that were retrapped within fourteen days of the first measurement. In addition, Figures 2.11 and 2.12 show the relationship between first and second measurements of bill length and depth in these birds. For all linear characters, short-term repeatability was over 90%. For wing and tarsus, which show a negligable seasonal variation (or parallel variation between birds),

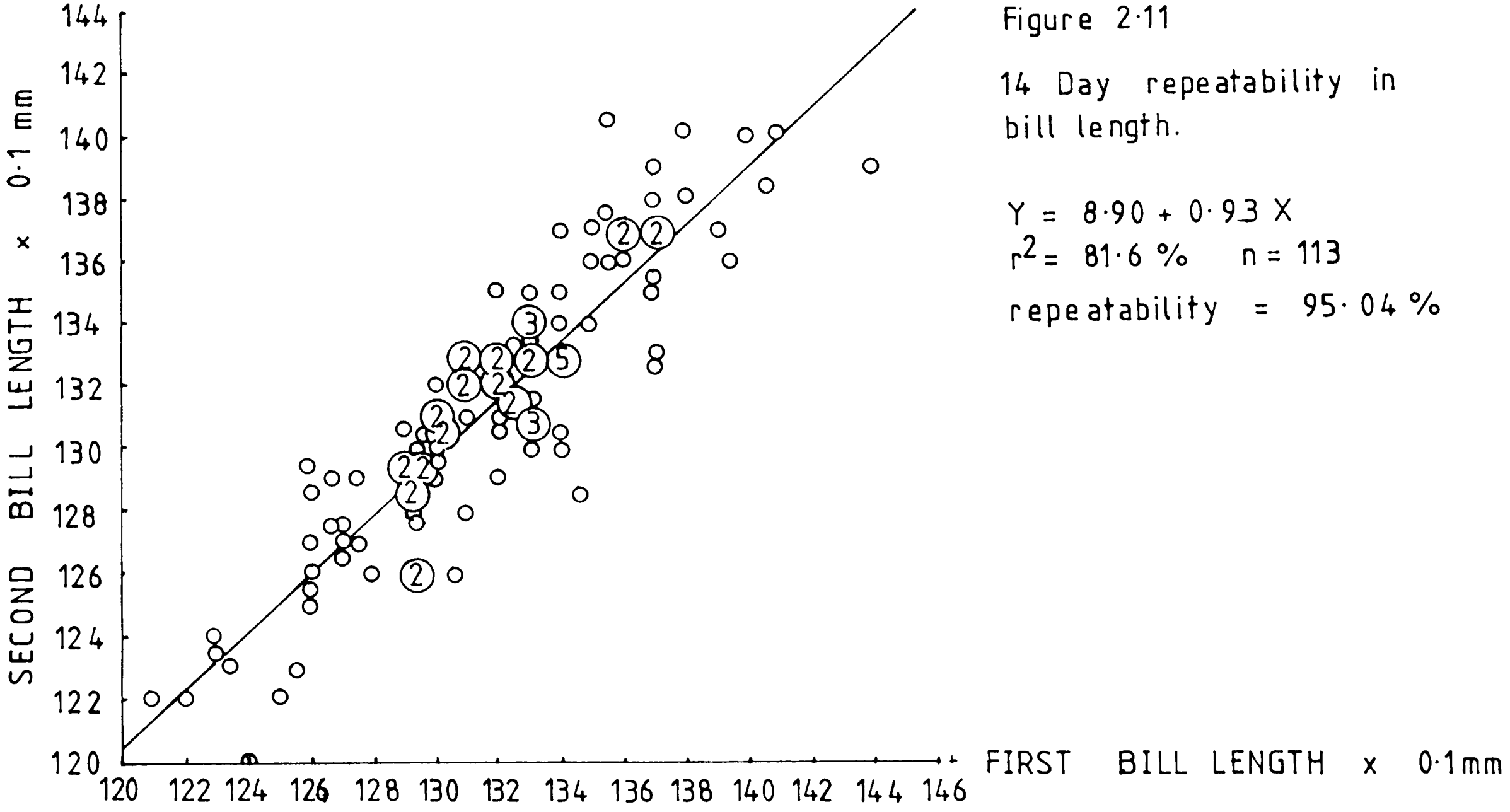


Figure 2·11

14 Day repeatability in bill length.

$Y = 8{\cdot}90 + 0{\cdot}93\ X$

$r^2 = 81{\cdot}6\ \%$ $n = 113$

repeatability = 95·04 %

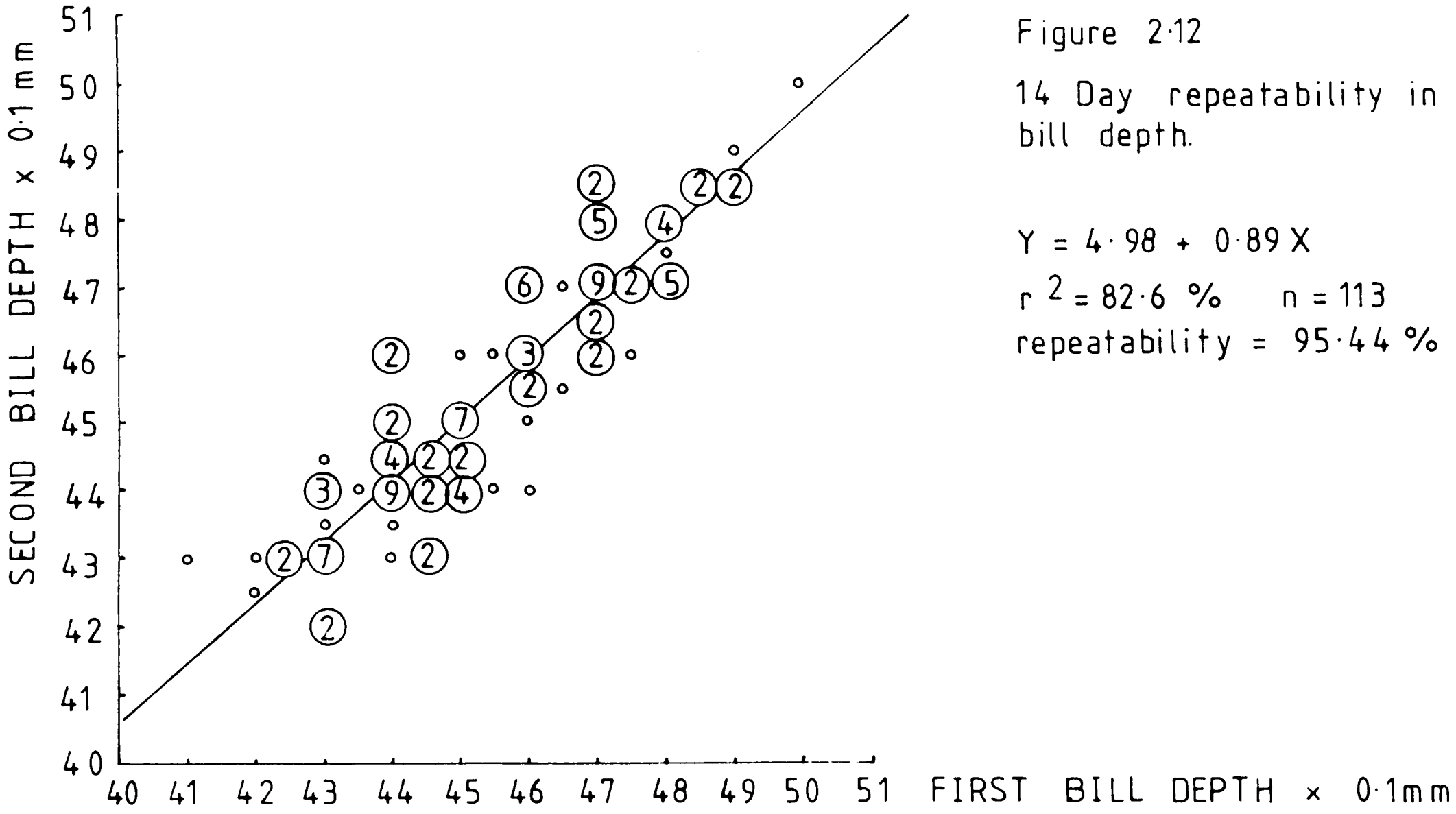


Figure 2·12

14 Day repeatability in bill depth.

$Y = 4 \cdot 98 + 0 \cdot 89 X$

$r^2 = 82 \cdot 6\ \%$ $n = 113$

repeatability = 95·44 %

Table 2.4 Short and long-term repeatability of measured characters. See text for details of repeatability calculation.

Character	Short-term (n=113)	Long-term (n=352)	Observer error
Tarsus	94.33 %	91.85 %	5.67 %
Wing	97.79 %	95.Ø6 %	2.21 %
Bill-length	95.Ø4 %	83.43 %	4.96 %
Bill-depth	95.44 %	88.35 %	4.56 %
Bill-index	94.13 %	84.41 %	5.87 %
Fat	56.15 %	66.98 %	Not Applicable *
Weight	84.68 %	84.39 %	Not Applicable *

* Note: Observer error is estimated as 1-(short-term error). This method is not applicable to characters such as fat score and weight which change markedly during short periods of time. This does not imply that these variables are measured without error. See Appendix 3 for further discussion of diurnal variation in fat and weight in the Great tit.

long-term repeatabilities were also greater than 90%. Bill characters showed a drop in repeatability over the longer period, suggesting a seasonal variation in these characters. Fat and body-weight showed lower repeatabilities as these variables are subject to diurnal and seasonal variation (Campbell and Lack 1985). The high short-term repeatability of bill characters indicates that the measurements taken were highly accurate, observer error being about 5% for all characters. Repeatability is discussed further in chapter 3.

Finally, it has proved impracticable to use colour-marking in the study of niche occupancy in the present study for a number of reasons. First, a colour marking project was already in operation in another part of Wytham at the start of the present study, leaving insufficient colour combinations free for this. Secondly, the suggestion that bill size might change seasonally (chapter 3) made colour marking according to bill size inappropriate.

2.4.2 Measurement of birds - Photographic methods.

To examine characters such as culmen curvature and the degree of abrasion received by the bill, a photographic method was developed. The apparatus, which was similar to that described by Van Noordwijk and Klerks (1982), is shown in Plate 1. It consisted of a single lens reflex camera ('Cosina CT-1G) fitted with a macro close-up lens and ring-flash unit, and mounted over a wooden base. The base acted as a mount for a 1 mm gridded background and reference mark for each exposure. The bird's head was held in a recess on the base. Lateral and dorsal exposures were then taken of a series of birds. Measurements (described later) were taken from the negatives using a low-power dissecting microscope fitted with a 0.1 mm eyepiece graticule.

2.5 Statistical analysis.

It is common practice for morphologists to carry out routine logarithmic transformations of biometric data (Boag 1983). This may be done for three reasons:

(1) The data may be skewed such that the log-transformed variables are normally distributed (required for parametric statistics).

(2) Heteroscedasticity may be removed for regression and ANOVA by transformation.

(3) There may be an allometric relationship between morphological characters.

Linear regression and correlation may be performed on the log-transformed variables if these co-vary linearly (Gould 1966). Smith (1980) pointed out that in the absence of these three statistical problems,

"there is no justification for routine log-transformations in morphological studies".

Morphological characters in the present study were normally distributed in every case (chapter 3). Smith (1980) and Harvey (1982) have shown that - although allometric relationships are often found between characters among taxa (Peters 1983), within species they are rarely found. Amadon (1959) showed that bill length in a range of species was not related allometrically to body size. Similarly, I found no evidence for allometric relationships among bill and body characters in the Great tit (chapter 3). Since allometry is the usual cause of heteroscedasticity in bivariate morphological relationships, I have found no necessity to routinely transform morphological data.

Original data are more meaningful to the reader than transformed values. Hence, in the univariate analysis of body weight, I have used original data (where necessary corrected for time of day etc.). However, since weight is a function of volume, whilst characters such as wing and bill length are linear, I have followed Amadon's (1943) recomendation and used the cube-root of weight in analyses among both types of variable. I have sometimes found it necessary to transform variables (non-morphological) to satisfy the conditions required for a particular statistical test. Where necessary, this is discussed in the appropriate place.

I have been aware of the complex interactions contributing to the variation in the characters studied. Hence, multivariate analyses (particularly multiple regression and partial correlation) have sometimes been used. However, where possible, the simplest statistical procedures have been used. Where necessary, to avoid 'weighting' the results of an analysis by repeatedly entering data from a retrapped individual within a season, multiple measurements of the same bird have been represented once only by the mean of all measurements of the bird made within that season. This avoids statistical problems associated with non-independence of the data. Data were analysed using the MINITAB statistical package (Ryan and Joiner 1981). All statistical analyses follow those of Sokal and Rholf (198) and Siegel (1956). Statistical significance has been accepted at a probability level of $P<0.05$, and levels of significance in tables are represented by the following convensions $P<0.05$ (*), $P<0.01$ (**), $P<0.001$ (***).

———————oOo———————

Chapter 3. Components of bill variation.

A description of bill variation in the Wytham Great tit population.

"...in further population studies in birds we will have to think not merely in terms of competition between individuals and pairs, but between sexes and age-classes too."

H.N. Kluijver, 1957.

Chapter 3. Components of bill variation. (A description of bill variation in the Wytham Great tit population.)

3.1 Introduction.

Kluijver (1957) pointed out the importance of individual differences in influencing population dynamics through competition. Similarly, in any morphological study, the total observed variation in a character may be broken down into a series of variance components which could be independent or could interact with each other. These components may also correlate with the variance components of the niche described previously (Christiansen & Fenchel 1977). Hence a proportion of the observed variation might be due to sex, age or to the growth environment. Each component may covary with variation in other morphological characters such as body size, and this correlation may itself reflect genetic (through linkage, pleiotropy etc) and/or environmental influences (such as the growth environment).

Further, the genetic and environmental components of phenotypic variation interact (Falconer 1981). For example, the genotype might predispose an individual in its choice of habitat, and different habitats may influence differentially the further development of the character. Sex or age-specific variation may themselves contain both genetic and environmental components. For example, if sexes occupy different ecological niches there may be different environmental factors influencing a character in each sex. This might be expressed through the environmental component of phenotypic variation. Further, the environmental influence on a character could be

seasonal and act differentially upon different classes of the population (age, sex etc) at different times. Hence it is necessary to determine the importance of sex, age and, where possible, genes for the characters under investigation. It might then be possible to correlate some part of the environmental variance to variation in measured environmental factors. This chapter attempts to describe the total variation in bill characters in the Wytham population in terms of its constituent variance components.

Despite the importance of variance components, a brief description of the total variation observed in the population is useful. Table 3.1 presents sample statistics for all morphological characters for all birds handled between 1982 and 1985. Note that the coefficients of variation for bill characters were greater than those for tarsus and wing length and for bill index - as variable as body weight. The latter is subject to considerable diurnal and seasonal variation (Owen 1954, Kluijver 1952). Hence, bill characters are amongst the most variable morphological characters in this species. Table 3.1 gives correlations among bill characters, body weight and tarsus length. However, these coefficients may be misleading since (as I shall show later) seasonal variation in both the bill and body weight confounds the true nature of these relationships. It should also be noted that the same results were obtained when these correlation analyses were repeated using logarithmically transformed measurements (bill length etc).

Table 3.1 gives an indication of the extent of sexual dimorphism in bill characters. Since the smaller sex has the longer bill, the difference is accentuated when bill length is standardised by dividing by the cube-root of body weight. In both sexes, 72% of the theoretical range of bill index (ie:minimum depth/maximum length to maximum depth/minimum length) was observed in the population. Noordwijk & Klerks (1983) found that 6.35% of

TABLE 3.1. Pooled sample statistics, comparisons and correlations for all characters recorded in the Wytham Great tit population, May 1982 - June 1985. All measurements are given in mm, weights in grammes.

MALES

CHARACTER	n	mean ± 1sd.	range	%c.v.
Bill length	848	13.31 ± 0.44	12.0 - 14.6	3.28%
Bill depth	849	4.60 ± 0.18	4.0 - 5.1	3.88%
Bill index	848	0.35 ± 0.02	0.288 - 0.397	4.61%
Tarsus len.	848	23.97 ± 0.63	21.0 - 27.0	2.61%
Wing length	852	76.7 ± 1.46	72.0 - 81.0	1.90%
Weight	853	19.22 ± 0.88	16.4 - 23.5	4.58%

FEMALES

CHARACTER	n	mean ± 1sd.	range	%c.v.
Bill length	778	13.36 ± 0.50	12.1 - 16.0	3.75%
Bill depth	778	4.39 ± 0.17	3.8 - 4.8	3.86%
Bill index	778	0.33 ± 0.02	0.270 - 0.386	5.24%
Tarsus len.	776	23.24 ± 0.62	20.5 - 25.5	2.66%
Wing len.	789	73.4 ± 1.44	66.0 - 78.5	1.95%
Weight	790	18.37 ± 0.97	15.6 - 22.2	5.28%

Sexes compared. (a) gives the t value and statistical significance for comparisons of mean values given above. (b) as (a) but after first standardising data by the cubed root of body weight. Note that sex differences were equally significant when the standardisation was made by tarsus length. (c) gives the difference between means as a percentage of the male value. Sample sizes for calculating degrees of freedom are as given above.

CHARACTER	(a)	(b)	(c)
Bill length	t= 1.79 P=0.074	t=10.89 P=0.000	0.30%
Bill depth	t=25.13 P=0.000	t=17.22 P=0.000	4.70%
Bill index	t=20.78 P=0.000	t=13.61 P=0.000	4.97%
Tarsus len.	t=23.83 P=0.000	t=12.06 P=0.000	3.07%
Wing length	t= 5.59 P=0.000	t=25.50 P=0.000	4.21%
Weight	t=18.62 P=0.000	not applicable	4.44%

Correlations among characters.

	MALES		FEMALES	
	cube rt. weight	tarsus	cube rt. weight	tarsus
Bill l.	0.248 P<0.05	0.246 P<0.05	0.293 P<0.01	0.177 NS.
Bill d.	0.328 P<0.001	0.003 NS.	0.201 P<0.05	-0.093 NS.
Bill i.	0.097 NS.	-0.171 NS.	-0.062 NS.	-0.195 NS.
Tars l.	0.303 P<0.01		0.303 P<0.01	
Wing l.	0.275 P<0.01		0.219 P<0.05	

Correlation between bill length and depth: males = 0.173 NS. females =0.037 NS.

Great tits on the island of Vlieland showed gross abnormalities of the bill. Many of these were environmental in origin, and resulted from damage. In the present study only 0.5% of birds showed such abnormalities.

Although this chapter is divided into sections by sex, age etc, it should be remembered that these sources of variation are not independent, but that they interact. For example, some consideration of age effects under the heading of sexual dimorphism has been necessary, and a seasonal component has been considered in all the analyses. I hope that this emphasises the integration of eco-morphological systems rather than confusing or misleading the reader.

3.2 Sexual dimorphism in bill characters.

3.2.1 Introduction.

Previous studies have shown sexual dimorphism in bill size in a range of passerine species (Selander 1966, Bock 1970, Burton 1974, Willson 1975). Rand (1952) suggested that sexual selection for body size might lead to sexual dimorphism in bill size through linkage or pleiotropy. However, he suggested that selection for bill size itself probably came about through competitive exclusion. Hence sexual dimorphism in bill size might reduce intraspecific competition in a shared environment. Rand also suggested that (unless sex-linked in some way) the extent of sexual dimorphism would be limited by the "hybridisation" between male and female. This hypothesis assumes that the environmental influences on bill size are similar for the two sexes. This may not be true. Schluter & Smith (1986) described differential selection for bill characters between male and female Song sparrows Zonotrichia melodia. Amadon (1959) also suggested that sexual dimorphism reflected sex-differences in the niche. He pointed out that since bill length did not increase allometrically with body size within a species, it was to some extent independent of body size.

The importance of absolute bill size has been implied by both the presence and the absence of sexual dimorphism in bill characters among different taxa. Snow (1953) found no sexual dimorphism in bill length in the Great tit although body size was highly dimorphic. Selander and Johnson (1967) and Johnson (1972) found the same result in the House Sparrow Passer domesticus. Both suggested that independence of bill and body size indicated the importance of absolute rather than relative bill size. Johnson (1966) found a

random geographical distribution in the extent of sexual dimorphism in bill length and depth amongst populations of flycatchers Empidonax spp. in California. He suggested that in some populations intraspecific competition might exceed interspecific and vice versa, but there was no clear pattern. Nor was there a clear case for character displacement.

However, most discussions of bill size in relation to sex demonstrate dimorphism. In most cases it is suggested (and in some cases demonstrated) that this also corresponds to a difference in the niche. Selander (1966) presented the definitive paper on the subject with a critical analysis of woodpeckers (Picidae). Hogstad (1976, 1978) found the same pattern of sex differences in both the niche and bill amongst four species of woodpecker in Norway. Fjeldsa (1981) suggested that dimorphism in the bills of grebes (Podicipedidae) allowed ecological segregation. Swennen et al. (1983) and Hulsher (1985) came to the same conclusion in their detailed analyses of bill variation in the Oystercatcher. Hespenheide (1973) suggested that sexual dimorphism should be greatest when food was either superabundant or very scarce. That is, character displacement by under- or over- utilisation. Hence most consider sexual dimorphism in bill characters to reflect a niche difference between sexes. Carlsson and Moreno (1983) found that in the Wheatear Oenanthe oenanthe male bill length was significantly greater than female bill length. The bill length determined how many prey items could be carried to the nest in each visit, with males carrying more prey than females. However, it is not clear how this might reduce competition since the prey brought by the two sexes seemed to be of the same size and species.

In the Medium Ground Finch Geospiza fortis on Isla Daphne Major, Galapagos, sexual dimorphism in bill characters was linked to a significant sexual dimorphism in body size with both bill and body size characters

strongly correlated (Boag 1983, Price et al. 1984).

In the Cape Verde Island Lark Alauda razae the difference between mean male and female bill length was 20.66% of the mean male bill length (Burton 1971). Soft X-ray photographs of this and of the bill of the extinct Huia Heteralocha acutirostris from New Zealand (perhaps the most dramatic example of sexual dimorphism in bill form) have shown that most of the dimorphism in bill length was due to variation in the rhamphotheca - there being little difference in the skeletal components of the rostrum (Burton 1974).

Willson et al. (1975) studied sexual dimorphism in bill length, depth and breadth in 66 species of North American land birds. They concluded that large species tended to be more dimorphic (absolutely) than small species. Grassland species were more dimorphic than forest or scrub species. The following figures were given for the percentage of species in each guild that showed significant sexual dimorphism:

Guild	Bill length	Bill depth	Bill breadth.
Bark users	80 %	-	-
Bark drillers	100 %	100 %	-
Ground gleeners	31 %	31 %	-
Foliage gleeners	25 %	25 %	-
High foliage users	-	12 %	-
Salliers	-	22 %	-

(Based on Willson et al. 1975)

They also found that resident species were more often sexually dimorphic than summer migrants. Comparisons among a further twenty four life-history parameters were not significant. They concluded that selection on or for the three characters occurred independently, so implying that they were not

generally correlated genetically. It should be pointed out that no allowance for body size was made in these analyses. That is, these are not measures of relative dimorphism but absolute dimorphism. Hence some of these results may be misleading.

The following three sections describe the extent of sexual dimorphism in the Wytham population. They also examine whether bill characters show seasonal variation in the degree of sexual dimorphism. I have shown above (Table 3.1) that at the population level (age classes and seasons pooled) sexual dimorphism in bill length and depth is highly significant in the Wytham Great tit population. In general, the mean female bill length exceeds the male's whilst the mean male bill depth exceeds the female's. Since Snow (1953) found no sexual dimorphism in bill characters, it has not been analysed previously in the Great tit. The present analysis of sexual dimorphism takes the following sequence. First, in section 3.2.2, I shall determine the relationship between variation in the rhamphotheca and that of the underlying skeleton, and to the skeletal component of body size. Secondly, in section 3.2.3, sexual dimorphism is considered within each season and within cohorts. Finally, in section 3.2.4, the relationship between bill size and body size is considered in more detail.

3.2.2 The skeletal bill size in relation to body size.

To determine the relationship between bill bone (nasal and premaxilla) size and body size, all available skeletons of *P. major* at the British Museum (Natural History) were measured. Sixteen complete skeletons of *P. m. newtoni* with the rhamphotheca removed were available for examination. The measurements taken (shown in Figures 3.1 and 3.2) were bill length and depth (taken as in the field and described above), maximum cranial length, breadth and height, length of the jugal bar, maximum sternum length, length of the tibiotarsus and tarso-metatarsus (tarsus in the field study). All were measured to 0.1 mm. Most of the characters showed significant inter-correlation (at least at $P<0.05$). and these data are shown in Table 1 of Appendix 2.

Three stepwise multiple regression analyses were carried out to determine the correlation between each bill character and the seven body size characters. The 'stepwise' method was favoured as the predictor variables were themselves highly inter-correlated and this method provided partialised r^2 values for each variable. However, the same results were obtained by a conventional multiple regression analysis. In the first analysis, bill length was entered as the criterion variable and the seven 'body size' variables as predictor variables. Only two characters predicted a significant part of the variance in bill length. Jugal length explained 70.65% of the variance, tibiotarsus length explained a further 9.93% (80.58% in total). The second analysis was carried out in the same way but with bill depth as the criterion. Again jugal length and tibiotarsus were the only significant predictors, explaining 47.67% and 10.13% respectively (57.8% in total). When all characters were entered, 85.7% of variance in bill length and

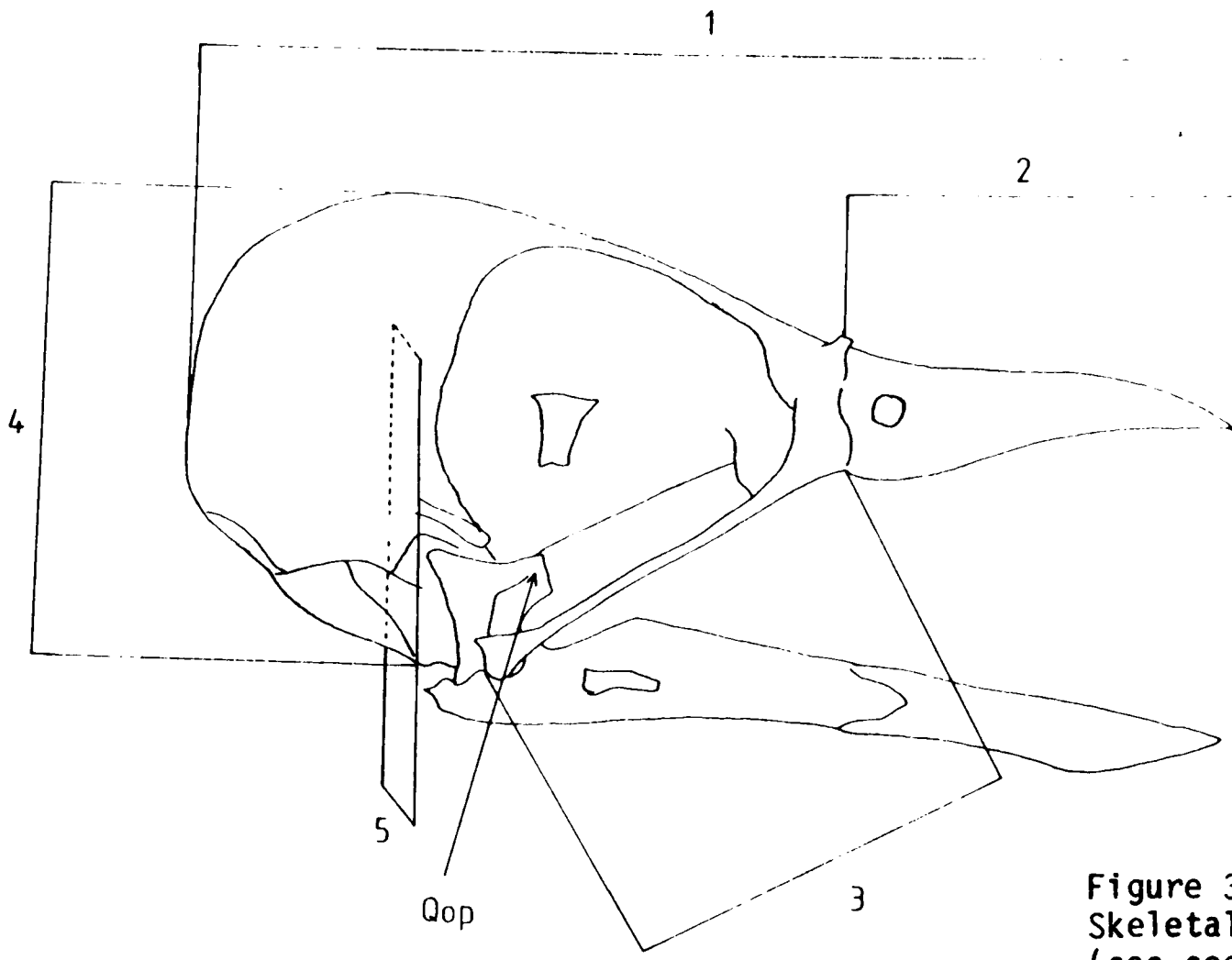


Figure 3.1.
Skeletal measurements of the head.
(see section 3.2.2.)

1 Maximum cranial length.
2 Bill length (as in the field).
3 Length of the Jugal bar.
4 Maximum cranial height.
5 Maximum cranial width.
Qop Orbital process of the Quadrate.

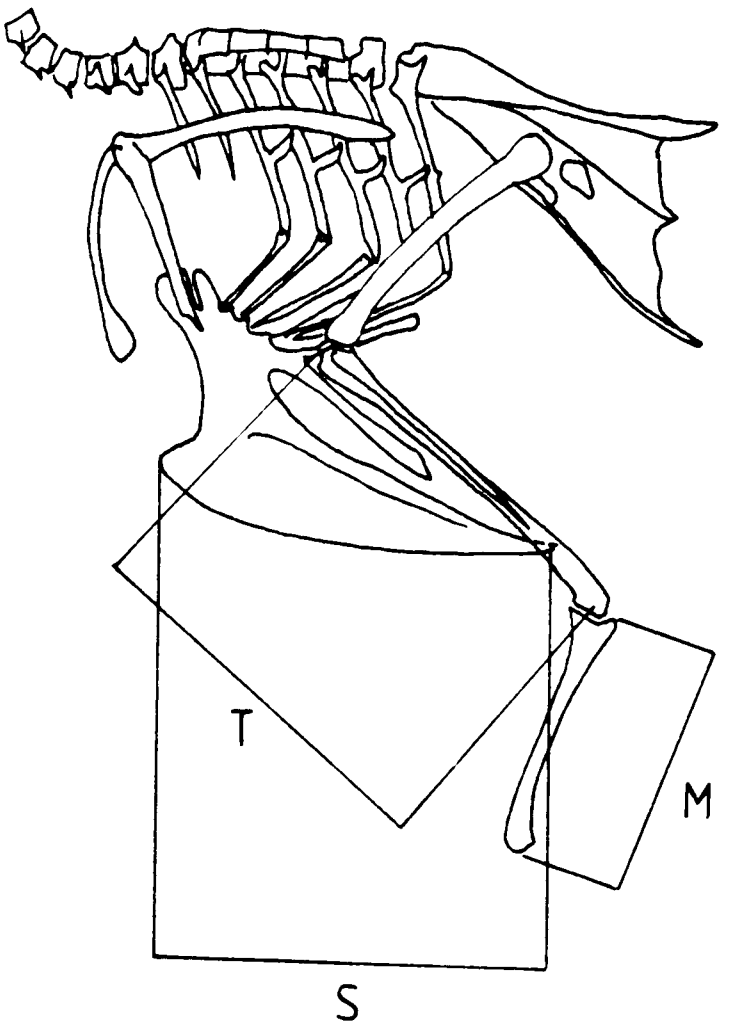


Figure 3.2.
Skeletal body measurements.
(see section 3.2.2)

M Length of Tarso-metatarsus.
S Maximum sternum length.
T Length of tibiotarsus.

68.07% of variance in bill depth were predicted by the seven body size characters. The corresponding multiple correlation coefficients of 0.925 and 0.825 for bill length and depth respectively were highly significant ($df=8$, $P<0.001$).

A third stepwise regression was carried out with jugal length as the criterion variable and all other variables entered as predictors. 88.67% of the variance in jugal length was explained by three significant predictors: bill length (13.36%), tarso-metatarsus length (70.88%) and tibiotarsus length (4.43%). The three cranial dimensions each explained less than one percent of the variance. Hence the length of the jugal bar is more closely related to the length of the bill and to body size than to the head size, indicating its structural importance to the rostral apparatus and possibly setting a constraint on bill (rhamphothecal) length.

In addition to the significant prediction of bill size by body size, bill length and depth were themselves significantly correlated ($r_{14}=0.920$, $P<0.001$), see Figure 3.3. Eight of the specimens had been sexed before preparation (3 male and 5 female). This small sample showed no significant differences in bill measurements. However, the correlations among bill and body characters in the whole sample predicts that males should have longer, deeper bills than females due to the difference in body size. The correlations obtained between bill length and depth separately for all males and females in the field study were very low (Table 3.1) and were significantly lower than that obtained for bone dimensions (for comparisons of Z-transformed correlation coefficients, $t_{\infty}=5.08, P<0.001$ for males and $t_{\infty}=5.57, P<0.001$ for females). Whilst one has reservations about results based on measurements of individuals from many populations, this analysis strongly suggests that the size of the rhamphotheca varies independently of the skeletal elements of the

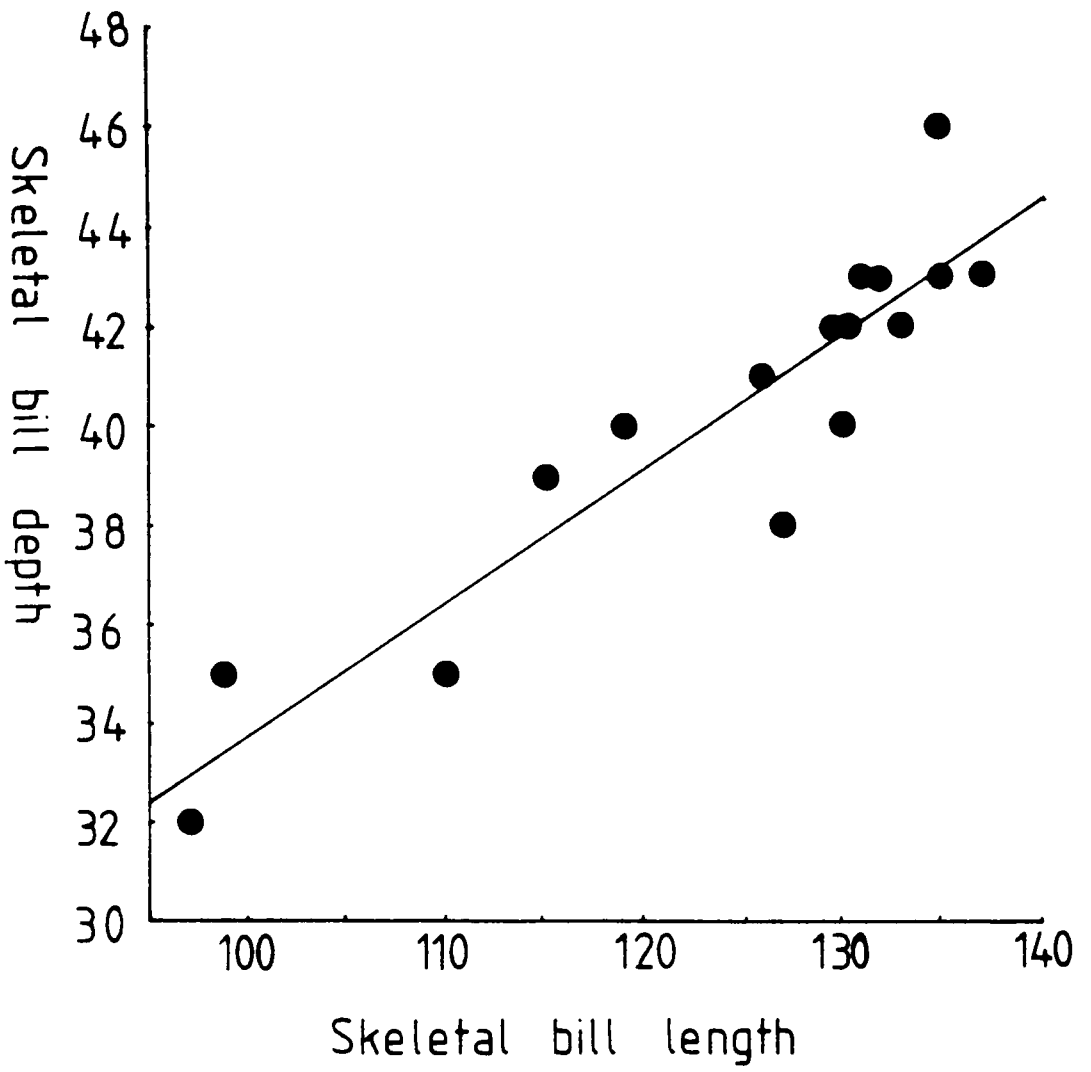


Figure 3.3. The relationship between bill length and depth in 16 complete skeletons of Parus major newtoni measured at the British Museum (Natural History). The regression line Y = 6.87 + 0.269 X was highly significant . r=0.921, P<0.001. Note: Scale is x 0.1 mm. for both measurements.

rostrum.

3.2.3 Sexual dimorphism in the Wytham Great tit population.

The following analyses are for Wytham field data. In section 3.6, I shall show that bill sizes in the Wytham Great tit population varied strongly with season within individuals. Therefore, the following examination of sex differences was carried out on data from within seasons. That is, data from different seasons have not been pooled. The statistical procedure followed has been to compare sexes with respect to each bill character within each season, and then to look for patterns of significance in the results so obtained. Although each comparison is a valid test for a significant difference within seasons (retrapped individuals were entered only once - see methods), some caution should be exercised when interpreting the overall pattern since samples from different seasons may not be wholly independent. I shall return to this later.

3.2.3a Sexual dimorphism in bill characters across age classes.

To analyse sexual dimorphism in bill characters they must first be standardised relative to body size (tarsus length). Since there is no evidence for an allometric relationship (see below) between bill and body size, bill characters were standardised by dividing each measurement by its appropriate tarsus length. This removes a substantial part of the sex-specific variance in bill characters that is due to a difference in body size (if the standardised values are then multiplied through by the combined mean of tarsus length, the result is equivalent to the residual bill dimension with

the tarsus covariance removed by regression). The standardised variables were normally distributed. Residents and the whole population were then analysed separately (residents are a more homogeneous sub-sample of the whole population). The sexes were then Compared with respect to each bill character by t test within these groups and within seasons.

Table 3.2 shows the results of these comparisons for each bill character. Of 60 such comparisons, only 12 (20%) results were not statistically significant. Of these, four cases showed significant sexual dimorphism in the whole population but not in the resident sub-set. This may have resulted from a sex and size bias in the immigrant population (see section 3.4) or there may be an ecological cause which will be considered in the final discussion. Seven non-significant comparisons occurred during the period Autumn/Spring 1983/84. This also will be considered in detail later. In all significant results, males had relatively shorter, deeper bills than females. Hence in general, the population showed considerable sexual dimorphism in bill characters and (since body size was largely removed as a source of variation) this was independent of the sexual dimorphism in body size. The exceptions to this pattern will be considered further later.

Table 3.2. Sexual dimorphism in bill characters in the Wytham Great tit population. For each season of the study (left margin), the table gives a t value for a comparison of males and females with respect to the bill character at the top line of the table. For each season and bill character, a t value is given for a comparison of residents only (R) and for the whole population (W). t values tended to be higher for the whole population (which contains residents) than for residents only. Levels of significance are indicated (in the usual way - see methods) for each t value and the degree of freedom for each test is indicated in the right margin.

t values for comparisons of males and females.

Season	sample	Bill-length	Bill-depth	Bill-index	d.f.
Summer 82	R	4.43 ***	2.11 *	3.27 ***	73
	W	5.74 ***	2.13 *	3.42 ***	131
Autumn 82	R	2.30 *	4.66 ***	3.48 ***	66
	W	3.44 ***	3.53 ***	2.05 *	101
Spring 83	R	4.68 ***	2.81 **	2.88 **	104
	W	6.33 ***	2.65 **	2.85 **	151
Summer 83	R	10.47 ***	1.30 n.s.	4.99 ***	144
	W	12.57 ***	0.81 n.s.	4.75 ***	233
Autumn 83	R	2.44 **	2.70 **	0.88 n.s.	125
	W	3.68 ***	3.10 **	0.48 n.s.	170
Spring 84	R	0.82 n.s	1.54 n.s.	0.13 n.s.	57
	W	1.99 *	0.14 n.s.	1.20 n.s.	99
Summer 84	R	6.95 ***	1.77 n.s.	2.36 *	114
	W	9.07 ***	2.41 *	4.02 ***	171
Autumn 84	R	2.47 **	6.29 ***	2.63 **	170
	W	4.15 ***	6.94 ***	3.01 **	293
Spring 85	R	1.48 n.s.	4.31 ***	3.35 **	55
	W	2.57 **	3.96 ***	2.84 **	114
Summer 85	R	6.19 ***	1.53 n.s.	2.17 *	71
	W	6.95 ***	2.68 **	4.11 ***	126

Note: Bill characters were standardised for body size before these comparisons were made (see text).

3.2.3b. An analysis of sexual dimorphism within cohorts.

The analyses described above suggested that the whole population showed more sexual dimorphism than the resident sub-population. More information is obtained if the same analyses are carried out within cohorts (defined by hatch year). This analysis was carried out on residents only. Table 3.3 shows the results of a series of t tests comparing males and females in each season with respect to each bill character and within each cohort. The analysis is therefore essentially similar to that in section 3.2.3a above, but includes an age component. It therefore provides somewhat more resolution than the previous analysis.

Analysed in this way, a seasonal pattern in sexual dimorphism emerges. Six out of seven comparisons of bill length made within cohorts in summer were significant. However, only two out of seven comparisons of bill depth in summer were significant. In Autumn, two out of five comparisons of bill length were significant whilst four out of five comparisons of bill depth were. No repeatable pattern was detected in Spring. This is summarised in Table 3.4. I have not carried out further statistics on these frequencies since they are not strictly independent when pooled. That is, some cohorts occur more than once in the analysis. However, even without further analysis, the results are highly suggestive, and two important points arise from them. First, the pattern of sexual dimorphism appears to be seasonal: in summer bill length tended to be dimorphic within cohorts whilst bill depth did not, and in Autumn the opposite was observed. Secondly, when taken with the results shown in table 3.2, indvidual bill characters varied in response to factors affecting the whole population and not the cohort alone. That is, an important part of the phenotypic variation was either age-specific or environmentally

TABLE 3.3. Sex differences in Great tit bill characters analysed within cohorts. Bill-length (BL), bill-depth (BD) and bill-index (BI) were standardised by tarsus-length. P values for t tests are given as in table 2.

COHORT hatch yr.:	1981			1982			1983			1984		
SEASON	BL	BD	BI	BL	BD	BI	BL	BD	BI	BL	BD	BI
Summer 82	**	*	***	HATCHED								
Autumn 82	n=5			*	***	**						
Spring 83	n.s.	*	* ***	n.s.	n.s.							
Summer 83	n.s.	n.s.	** ***	n.s.	***	HATCHED						
Autumn 83			*	**	n.s.	n.s.	n.s.	n.s.				
Spring 84			n.s.	n.s.	n.s.	n.s.	n.s.	n.s.				
Summer 84			**	n.s.	n.s.	***	n.s.	n.s.	HATCHED			
Autumn 84						n.s.	*	n.s.	n.s.	***	n.s.	
Spring 85						n.s.	**	***	n.s.	*	*	
Summer 85						***	n.s.	n.s.	**	**	**	

Table 3.4 The number of cohort-seasons in which bill characters showed significant sexual dimorphism in the Wytham Great tit population. The number of comparisons (of sexes in a cohort, in a season) made is indicated by (n).

Character	Summer (n=7)	Autumn (n=5)
Bill length	6	2
Bill depth	2	4

determined (or both) since the degree of sexual dimorphism changed within cohorts between seasons. Age-specific effects are considered in section 3.3 whilst environmental influences generally are discussed in sections 3.5 to 3.7.

3.2.4 The correlation between bill characters and body weight.

Table 3.1 suggests that bill characters and body size (indicated by tarsus length) were uncorrelated, and that in general the correlation between bill dimensions and body weight was poor (r^2 never more than 11%). Although this indicates that the correlation between bill and body size was weaker than in the skeletal elements, it may be misleading because of the possible confounding influence of season. To overcome this I first divided the whole population into first-year and adult males and females. Correlations were then calculated between $3\sqrt{\text{body}}$ weight and each bill character in each age and sex class within each season. The results are summarised in Table 3.5. Full results are given in appendix 2.

In general the correlations between bill characters and body weight were again poor. Of 117 calculated correlations (one sample contained only two individuals and was ommitted from the analyses - see Appendix 2) only 27 were significant at or below $P<0.05$. Of these, 14 were significant at $P<0.05$, nine at $P<0.01$ and four at $P<0.001$. However, this is considerably more significant results than would be expected by chance alone (that is type 1 error). Age and sex did not appear to influence the correlation. However, in winter, the occurrence of a significant correlation between bill depth and body weight was associated with whether the birds were measured during a season when beech

TABLE 3.5 The number of correlation coefficients between bill characters and the cube-root of body weight of Great Tits that were significant in analyses carried out on data within age and sex classes (see text) and within seasons. Only Wytham-hatched birds were used in the analyses. Note: the autumn sample is 11 not 12 as only 2 Wytham-hatched adult females were trapped in the autumn of 1982 (see Appendix 2).

CHARACTER	SUMMER		AUTUMN		SPRING		TOTAL	
	*n	n sig	n	n sig	n	n sig	n	n sig
Bill length	16	1	11	6	12	3	39	10
Bill depth	16	5	11	6	12	2	39	13
Bill index	16	0	11	2	12	2	39	4
Total:	48	6	33	14	36	7	117	27

* NB: n is the number of correlation coefficients calculated for the season in each character, hence the 16 correlations used in summer represent first-year and older males and females (4 categories) in each of 4 summers = 16. Similarly in Spring n=12 for the same four categories over three springs, but see note above for autumn.

mast was a major part of the diet (more than 80% of Great tit observations on beech mast - see section 2.3). To test this, a 2x2 contingency table was set up with the number of significant versus non-significant correlations as one contingency, and whether the birds were feeding on or off beech mast as the other. The Fisher exact probability of an association calculated for this was P=0.001. To test that this association was not an artefact of differences in sample size (since the same coefficient of determination would show different levels of significance with different degrees of freedom) I repeated this analysis but defined the first contingency as a correlation coefficient above or below an arbitrary value of 0.5 (r^2=0.25). The Fisher exact probability was still significant at P=0.01. In the first winter of the study, the birds did not feed on beech mast until the Spring (Figure 2.9). Hence the 'beechmast feeding' seasons consisted of two Autumns and one Spring. This suggests strongly that the association did not result from a seasonal difference independent of mast foraging. See Appendix 2 for the full table of results used in these analyses.

Finally, Correlation coefficients were calculated between bill length and depth in each of the age, sex and season categories used above. Of 39 correlation coefficients used (one sample omitted as above), ten were significantly different from zero: six in summer and four in autumn. The autumn correlations were each significant at P<0.05 whilst two summer correlations were significant at P<0.01 and two others at P<0.001. Rather more correlations in summer were significant than might be expected by type 1 error so there is some tendency for bill length and depth to be correlated then. Of the ten significant correlations, nine were significantly lower (tested by t test on z transformed correlation coefficients) than the correlations observed between the corresponding skeletal dimensions.

3.3 Age-specific variation in bill characters.

3.3.1 Introduction.

Polis (1984) used Christiansen & Fenchel's (1977) model of niche breadth to examine age-specific niche variation in scorpions. He found that the difference in size among age-classes of scorpion led to differences in prey size, and suggested that this simple relationship could result in ecological segregation. Little has been written on bill variation among age groups of full-grown birds. The highly specialised bills of Crossbills Loxia spp. are not fully developed until some 8-9 weeks after hatching. Consequently they are dependent upon the parents for considerably longer than other finches of a comparable size (Nethersole-Thompson 1975). However, in general, differences between juveniles and full-grown birds may be trivial in an ecological context.

Selander & Johnson (1967) found that in House Sparrow populations in North America, adults of both sexes were significantly larger in bill length and depth than first-year birds collected at the same time. However, since first-year birds were recognised by incomplete cranial ossification (Svensson 1975) it is possible that the bill also was not fully grown. In many long-billed species of wader (Charadrii), first-winter birds have shorter bills than adults (Prater et al. 1977). Since bill length may set a constraint on feeding in these birds, this may lead to ecological differences among age-classes. However, a distinction should be made between age-differences arising from simple differences in growth and development, and age-differences observed after the full size of the bill has been attained. Either might relate to differences in ecology among age-groups, but it is more

difficult to establish whether the difference is adaptive if it is the necessary consequence of incomplete development. Swennen et al. (1983) and Hulscher (1985) found significant differences between age classes of Oystercatcher Haematopus ostralegus. These correlated with differences in ecology and were not due to simple differences in growth.

3.3.2 Age-specific bill variation in the Wytham Great tit population.

I have shown that within seasons, the degree of sexual dimorphism varied between cohorts in the Great Tit. This could have arisen through directional selection. However, in chapter 7 I shall show that this is probably not the case. Hence I suggested (section 3.2.3b) that age differences might explain part of the variation among individuals. A number of plumage characters vary with age in the Great Tit. Van Balen (1967) showed that wing length increased with age (although Bjorn (1960) found that this was not the case in all populations), and Perrins (1979) noted that plumage tends to become brighter. Most important for the present study, O'Connor (1973) showed that bill size was full-grown 6 weeks after hatching so that since the rhamphotheca undergoes continual replacement, there is no a priori expectation of an age-specific component of bill variation.

To examine the influence of age on bill size I have used only Wytham-hatched individuals since their ages were exactly known. This comprised a total sample of 998 handlings, 573 male (334 individuals) and 425 female (271 individuals). When an individual was measured more than once in a season, it has been represented once only, by the mean of those measurements, as was described in the methods (chapter 2). However, in practice, most data have

been used since relatively few recaptures occured during the same season of analysis.

For these samples I have carried out two series of comparisons. First, within each season's data, single factor ANOVAs were carried out separately for bill length and depth within each sex with age as the determining factor - a total of 40 ANOVAs. Further I have compared first year with older birds in the same groupings by t tests. This tests whether a significant ANOVA resulted from a systematic change in a bill character with age. Of 20 ANOVAs carried out on female data, only one was significant at $P<0.05$, which may be expected by chance. No t tests of females were significant. In males, 5 ANOVAs were significant and these were also significant in t test comparisons (see Table 3.6).

Secondly, within sexes and seasons, bill measurements were expressed as deviations from the seasonal mean. Standardised values were then pooled across years within the three season types (autumn, summer and spring) and ANOVA and t tests carried out as before. Again, age was unimportant in females and in summer, males showed no significant age effects. In autumn, a slight effect was detectable on male bill depth but this was not systematic (see table 3.6). In spring however, both bill length and bill index were strongly and systematically influenced by age. Older birds had shorter and therefore relatively deeper bills than younger birds.

Since some birds entered the analyses in more than one season (in different age classes), these results cannot be used to identify systematic changes in bill dimensions with age. However, they may be used to examine age-specific variation within seasons, and since age effects were either very weak or absent in autumn and summer but strong in the intermediate season, and since older birds had absolutely shorter bills than younger individuals, I conclude

Table 3.6 Age effects on male bill characters within seasons. The table gives ANOVA and t test results for the second series of analyses - see text for details.

	BILL LENGTH	BILL DEPTH	BILL INDEX	D.F
AUTUMN	F=1.13,ns	F=2.85 *	F=1.74,ns	3,216
	t=-Ø.46,ns	t=1.85,ns	t=1.94,ns	218
SPRING	F=4.Ø9, **	F=1.42,ns	F=3.Ø2, *	3,137 see below
	t=-2.81,**	t=1.37,ns	t=3.Ø4,**	139
SUMMER	F=1.64,ns	F=Ø.67,ns	F=1.8Ø,ns	4,2Ø3
	t=-Ø.Ø2 ns	t=Ø.25,ns	t=Ø.18,ns	2Ø6

that age-determined bill variation (especially resulting from growth) is insignificant in both sexes. Age was not a contributor to bill variation in females, but was important in males in spring (Table 3.7).

Table 3.7 Age variation in bill length among male Great tits in Spring.

Age (EURING CODE)	n	mean bill length	± 1 s.d.
1st spring (5)	81	131.9	3.7
2nd " (7)	39	130.5	3.9
3rd " (9)	17	130.1	3.0
4th " (11)	4	126.5	4.0

$F_{(3,137)}=4.09$ **

3.4 Residents and Immigrants.

3.4.1 Introduction.

Bulmer (1973) showed that approximately half (46% of males, 58% of females) of the breeding Great tit population of Wytham were hatched in nests in natural sites (or at least not from Wytham nest boxes). Since the percentage of natural sites used in the Wytham population is very small (probably less than 5% of nests in most years), in practice this means that about half the population are immigrants (Perrins 1979, Clobert et al. in prep.). Webber (1975) showed that the rate of immigration depended partly upon the density of birds already in the population, and that this was correlated with the quality of the beech crop. This suggested that immigration and emigration were not in equilibreum but that Wytham acted as a 'sink' for dispersal from outside. This is perhaps not surprising since the woodland habitats of Wytham are more suitable for tits than the surrounding fields and hedgerows (Krebs 1971). With so high a rate of gene flow into the population, one might not expect immigrants and residents to differ genetically unless immigrants that were able to settle were a strongly selected group. That is, if settlers were more like residents than the rest of the immigrant population from which they had come. However, if this were true, the sampling of immigrants within Wytham might itself be strongly biassed so that no differences might be found even if present in the immigrant population as a whole. Greenwood et al. (1979) found a significant tendency for immigrants and residents to select mates from the same classes (ie: immigrant or resident). However, assortative mating of this kind is unlikely to maintain existing differences in quantitative characters within the

population since the progeny of all Wytham pairings are residents by definition so that genetic introgression would be expected (at least in quantitative traits such as bill length).

Therefore, any morphological differences found between between immigrants and residents are more likely to arise from differences in the environmental component of phenotypic variation. These might arise from differences in the nestling growth environment, or from environmental differences operating during adult life (which might be termed 'immediate') sources of variation. Since the growth environment is more uniform for broods in nest boxes (notwithstanding differences in food abundance among territories), if this were a cause of differences in the environmental component, we should expect immigrants to vary more than residents. Further, where present, this difference is more likely to influence <u>hard</u> than <u>soft</u> morphology (see glossary) since the latter is more strongly influenced by immediate causes of variation. For example, Garnett (1976) showed that the tarsus was full grown at fledging in the Great tit. Hence if tarsus length varies more among immigrants than among residents it is either due to variation in the growth environment or because residents are generally more closely related to each other than immigrants are. However, the rhamphotheca grows and wears continually and is 'mounted' on a skeletal base that is itself not fully grown until some weeks after fledging (O'Connor 1973). Hence if immigrants (or residents) varied more in bill characters, the difference cannot be readily attributed to a specific cause.

Webber (1975) showed that most immigrants were first year birds at the time of immigration, and suggested that most immigration occurred during post-natal dispersal before their first October. Hence differences in soft morphology between immigrants and residents should only occur if the two

groups occupy different niches such that the difference in niche directly contributes to the morphological variation. It is of course possible that differences in morphology already exist which could result in differential habitat selection. Hence three questions arise concerning immigrants and residents. First, do immigrants and residents differ in their means in any systematic way? and if so, which age or sex groups differ. Secondly, do they differ in relative variance? Thirdly, is there any evidence for differential niche occupancy between the two groups?

3.4.2 The comparison of immigrant and resident Great tits in the Wytham population.

To test for a systematic difference between immigrant and resident groups, the population was sub-divided by age (first-year or older), sex and season. For each character (bill length, bill depth, tarsus and wing length) immigrants and residents were compared by t tests within their sub-groups (age,sex etc). Although tedious, this method avoids complications caused for multiway ANOVA by having unequal replicates and different variances. Of 160 comparisons (2 ages x 2 sexes x 4 characters x 10 seasons), only nine were significant. Six were significant at $P<0.05$, three at $P<0.01$. The significant results are summarised in Table 3.8. Since eight tests significant at $P<0.05$ and one (1.6) at $P<0.01$ were expected by chance alone (type 1 error), there is little evidence for a systematic difference between immigrants and residents. However, the mean dimension of residents exceeded that of immigrants in eight of the nine significant results. The probability of this by chance (binomial test) is 0.0176. This suggests a tendency for residents to exceed immigrants in body dimensions. Similarly, seven of the nine results

Table 3.8 A summary of the significant differences observed between immigrant and resident classes of Great tit. 1Y = first year, Ad = adult, R = resident, I = immigrant, Bl = bill length, Bd = bill depth, T = tarsus, W = wing length, M = male, F = female.

Season	year	character difference	significance.
Summer	1983	1Y M R Bd > I Bd	**
	1984	Ad M R Bd > I Bd	*
	1985	Ad M R T > I T	*
Autumn	1983	Ad M R W > I W	*
	1984	Ad M R Bd > I Bd	*
	1984	R T < Ad F I T	*
Spring	1984	Ad M R Bl > I Bl	**
	1984	Ad F R Bl > I Bl	**
	1985	1Y F R T > I T	*

concern adults and the probability of this is 0.07 so that there might sometimes be a difference between these groups, but the effect is very weak.

To test for a systematic trend in variation, the coefficient of variation of each character was calculated for each sex in each season. The coefficients for each character for residents and immigrants were then simply scored as larger or smaller for each of the twenty cases (2 sexes by ten seasons). The binomial probability of obtaining such a frequency by chance was then calculated for each character. It is assumed that coefficients of variation are independent between seasons. For bill characters this is supported by the results themselves which showed no systematic difference in variation between groups. These results are shown in Table 3.9.

Table 3.9 suggests a tendency for tarsus length to vary more among immigrants than among residents. It is important to note that although tarsus length showed some evidence of a systematic difference in variance, in the same samples of birds, bill characters did not. For tarsus length, These results accord with the prediction based on a difference in growth environment (or mean relatedness within the two groups) rather than differences in the immediate environment. When variance ratio tests were carried out on these data (for all characters), not one comparison of bill characters (40 comparisons) between residents and immigrants was significant and only three tarsus variance ratios were significant. One (males in Autumn 1984) at $P<0.05$ might be expected by chance (20 tests), and two (both males and females in Spring 1985) at $P<0.01$. But in both the latter cases the immigrant variance was significantly lower than the resident's. It is not clear why this should be. For bill characters, not one variance ratio test gave a significant result.

The final question relates to niche occupancy. This is difficult to answer

Table 3.9. Binomial comparison of immigrant and resident coefficients of variation (c) tested within sexes and seasons. I = immigrant, R = residents. The table shows the number of seasons in which the coefficient of variation for immigrants exceeded that of residents and in which residents exceeded immigrants, irrespective of whether the variances differed significantly.

	Comparison of c			
Character	I > R	R > I	n	P
Bill length	10	10	20	0.176 NS
Bill depth	10	10	20	0.176 NS
Tarsus	14	6	20	0.037 *
Wing	11	9	20	0.160 NS

since for logistic reasons it was not possible to follow known individuals in this study (see methods). However, some attempt may be made to investigate this by comparing capture rates and relative frequencies of immigrants and residents in different habitats. This analysis relates only to winter trapping since the relative frequencies of residents and immigrants breeding in different woodland habitats will be considered in chapter 6. First, the population was divided by age and sex classes within seasons as before. Within these subgroups, the retrap frequency distributions (as Fig. 2.5) for immigrants and residents were calculated and compared by Mann-Whitney U tests. Of 40 such tests (2 ages by 2 sexes by 10 seasons) not one was significant. A summary of the distributions is presented in table 3.10 in which data are pooled within "autumns" and "springs". This analysis shows that winter trapping rates are essentially the same for immigrants and residents.

Secondly, trapping sites were divided into baited and un-baited sites. Then, the frequency of capture of residents and immigrants was compared as a 2x2 X^2 contingency table within age and sex classes and within autumns and springs. Table 3.11 shows the capture frequencies used in these tests. Note that across the whole period of the study, less than 5 individuals were trapped at both a baited and an unbaited site in the same season so that the contents of cells in the chisquare contingency tables may be regarded as independent.

There is little evidence that residents and immigrants differ morphologically or behaviourally in terms of their relative use of different trap sites or risk of capture. There is some indication that the variance of characters which develop fully in the nest is higher in immigrants than residents. This is presumably due either to the greater variation in nest site

Table 3.1Ø. Retrap distributions for resident and immigrant Great tits subdivided by age and sex within season type. 1Y = First year, Ad = Adult. M = Male, F = Female.

Autumn

Capture	1Y M		Ad M		1Y F		Ad F	
f/ group:	imm	res	imm	res	imm	res	imm	res
1	24	88	24	44	59	69	22	31
2	4	12	4	6	9	13	4	5
3	2	6		4	3	1	1	2
4	1	2	1	1				
5				2				
N indiv's	31	1Ø8	29	57	71	83	27	38

Spring

Capture	1Y M		Ad M		1Y F		Ad F	
f/ group:	imm	res	imm	res	imm	res	imm	res
1	22	56	12	23	42	34	16	16
2	2	9	4	11	5	3	13	5
3		2	1	4		1		
4	1	1		1				2
5		1	2				1	
N indiv's	25	69	19	39	47	38	3Ø	23

Table 3.11. Capture frequencies of immigrant and resident Great tits at baited and un-baited trap sites at Wytham in Autumn and Spring 1982-1985.

Autumn		Baited	Unbaited	$X^2_{(1)}$	
1Y F	imm	30	57	2.083	NS
	res	44	54		
1Y M	imm	21	31	0.278	NS
	res	1	2		
Ad F	imm	8	23	0.424	NS
	res	16	33		
Ad M	imm	16	20	0.459	NS
	res	42	40		

Spring		Baited	Unbaited	$X^2_{(1)}$	
1Y F	imm	32	19	0.852	NS
	res	35	14		
1Y M	imm	18	12	1.336	NS
	res	60	24		
Ad F	imm	26	9	0.254	NS
	res	27	7		
Ad M	imm	24	9	2.168	NS
	res	52	9		

conditions experienced by the immigrant group or to their lower mean relatedness. However, with regard to bill morphology, immigrants and residents may be considered as similar (ie: drawn from the same statistical population).

3.5 Growth and development of the bill.

I have shown that by autumn first-year Great tits differ little (if at all) in bill size from adults. Indeed in spring bill length was significantly greater in first-year males than in adults. Hence - as reported by O'Connor (1973) - the bill is fully developed by the first autumn . Further, by autumn first-year birds showed as much sexual dimorphism as adults. I have suggested that the growth environment may contribute more to the variance in hard morphology than to that in soft. This section examines the contribution made by the growth environment to the variation in bill characters.

In 1984, bill depth was measured (as in adults) in 433 fifteen day old nestlings, that is all nestlings in each of 63 nests. These birds were also weighed, but were not sexed (see chapter 2). Parent bill measurements were available for 60 of these nests. Figure 3.4 shows the distribution of bill depth in these nestlings. Figure 3.4a shows the distribution of observed measurements, whilst figure 3.4b shows these data standardised between nests as deviations from the within-brood mean. That is, removing the variation due to differences between nests. Calculated normal curves have been fitted to the distributions and these also are shown in the figures. Both distributions are normal although the standardised variates show a slightly platykurtic distribution. The mean bill depth for all nestlings was 3.83 $\pm$ 0.16mm (c.v.=4.2%). A single classification ANOVA was carried out to determine the proportion of variation in bill depth that was due to differences among nests. The ANOVA table is given as Table 3.12. 25.12% of the total variance in bill depth was attributable to differences among nests and this was highly significant. This variance includes all nest-effects, including differences

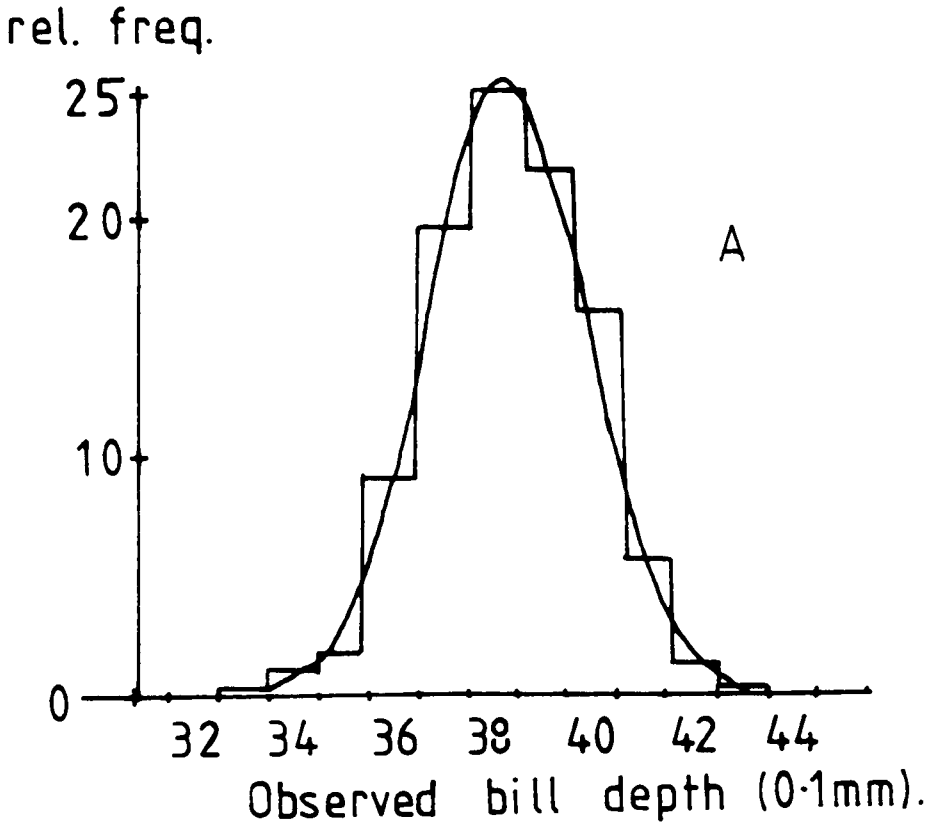


Figure 3.4. A - (upper figure). The relative frequency distribution of bill depth in 433, 15 day old Great tit nestlings measured during the summer of 1984. A calculated normal curve has been fitted to the distribution.

B - (lower figure). Relative frequency distribution as above, but measurements were expressed as deviations from the brood mean. This procedure removes that part of the variation represented by differences in the means between broods. The two figures are essentially similar.

Table 3.12. Analysis of variance on bill depth in 433 fifteen day old Great tit nestlings from 63 nests measured in 1984.

Source of variation	d.f	s.s	m.s	F	P
Nests	62	282.43	4.56	2.ØØ	<Ø.ØØ1
Error	37Ø	841.73	2.27		
Total	432	1124.16			

in broods size. Since the nestlings were not sexed the proportion of variance due to sex is derived by inference in the next section.

In 1985 bill length, depth and gape width were recorded in samples of nestlings of different age. Gape width was taken at the widest point of the gape flange. The flexibility of this structure introduces some measurement error. Bill length was taken as exposed culmen (see glossary) as the standard method was impracticable for very small nestlings. Figure 3.5 shows the relationship between the two bill length measurements (ie: exposed culmen versus the standard method) in fifteen day old nestlings. The regression line may be used to compare these data with those for the fully-grown bill measured after fledging. For logistic reasons it was not possible to follow the development of individual nestlings. Hence two nestlings (taken at random) were measured in each brood when encountered during routine nest inspections. Table 3.13 shows the sample sizes available for nestlings of a given age.

Figures 3.6, 3.7 and 3.8 show the change in bill dimensions with age in these nestlings. Since the data come from different individuals, growth curves have not been fitted. However, the figures clearly show a linear increase in bill length (as was found in the Blue tit by O'Connor 1975), while bill depth shows a more convex growth pattern.

Growth rates differ markedly between metric characters within individual birds - characters essential to the young chick developing ahead of those of importance only when older. Hence in altricial passerines, the digestive tract and associated organs develop most rapidly. Tarsus length increases rapidly also to provide stability and a greater height of reach to the begging chick. Characters such as wing-length which are of no importance to a young

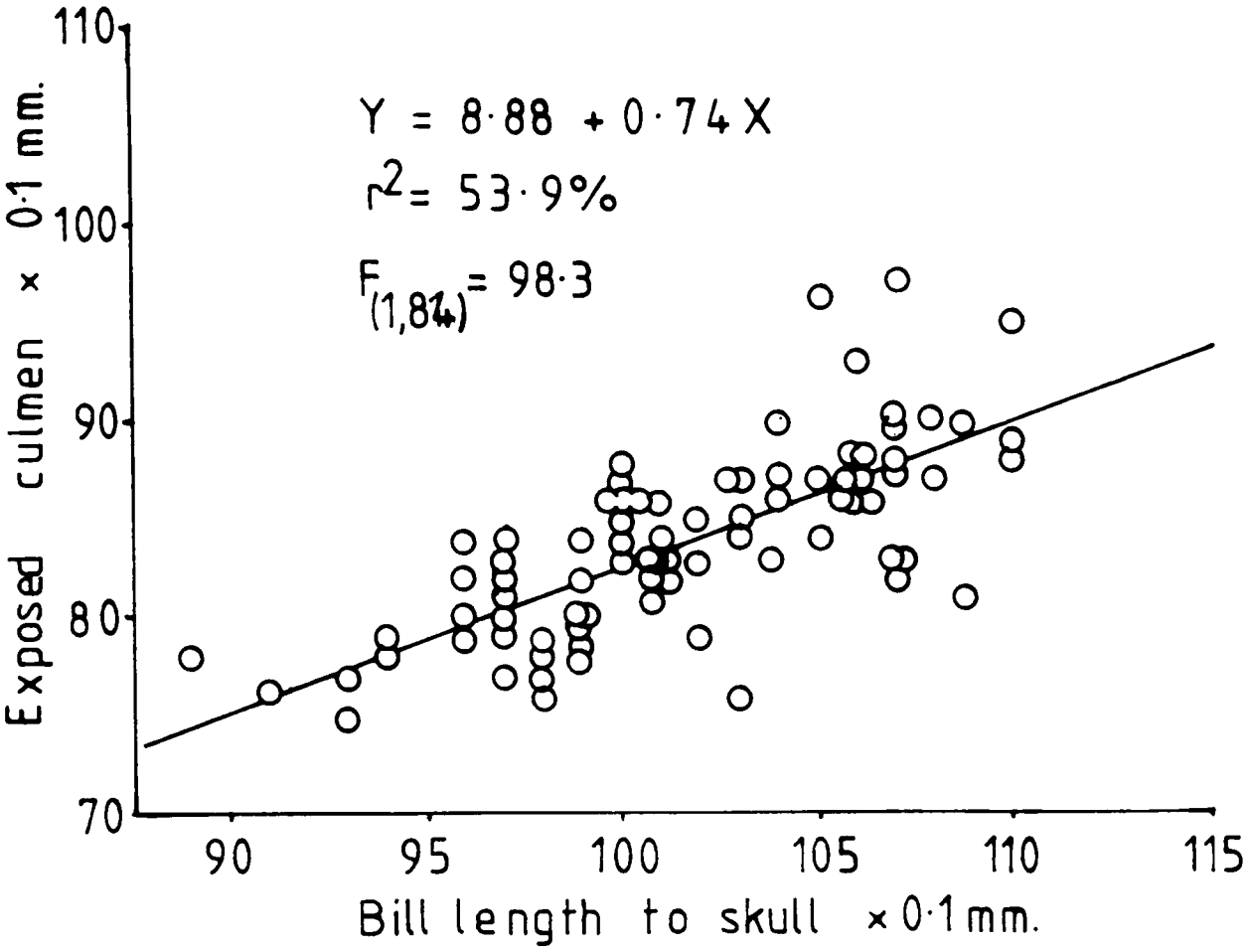


Figure 3.5 The relationship between 'exposed' culmen bill length and the 'standard' bill length measurements taken from all 15 day old nestlings measured in 1985 (n=86).

Table 3.13. Nestling sample sizes available for bill measurement at different ages.

AGE (days).	N nests.	N nestlings.
1	1Ø	2Ø
2	1Ø	2Ø
3	4	8
4	7	14
5	7	14
6	9	18
7	8	16
8	6	12
9	8	16
1Ø	6	12
11	3	6
12	7	14
13	9	18
14	5	1Ø
15	44	88

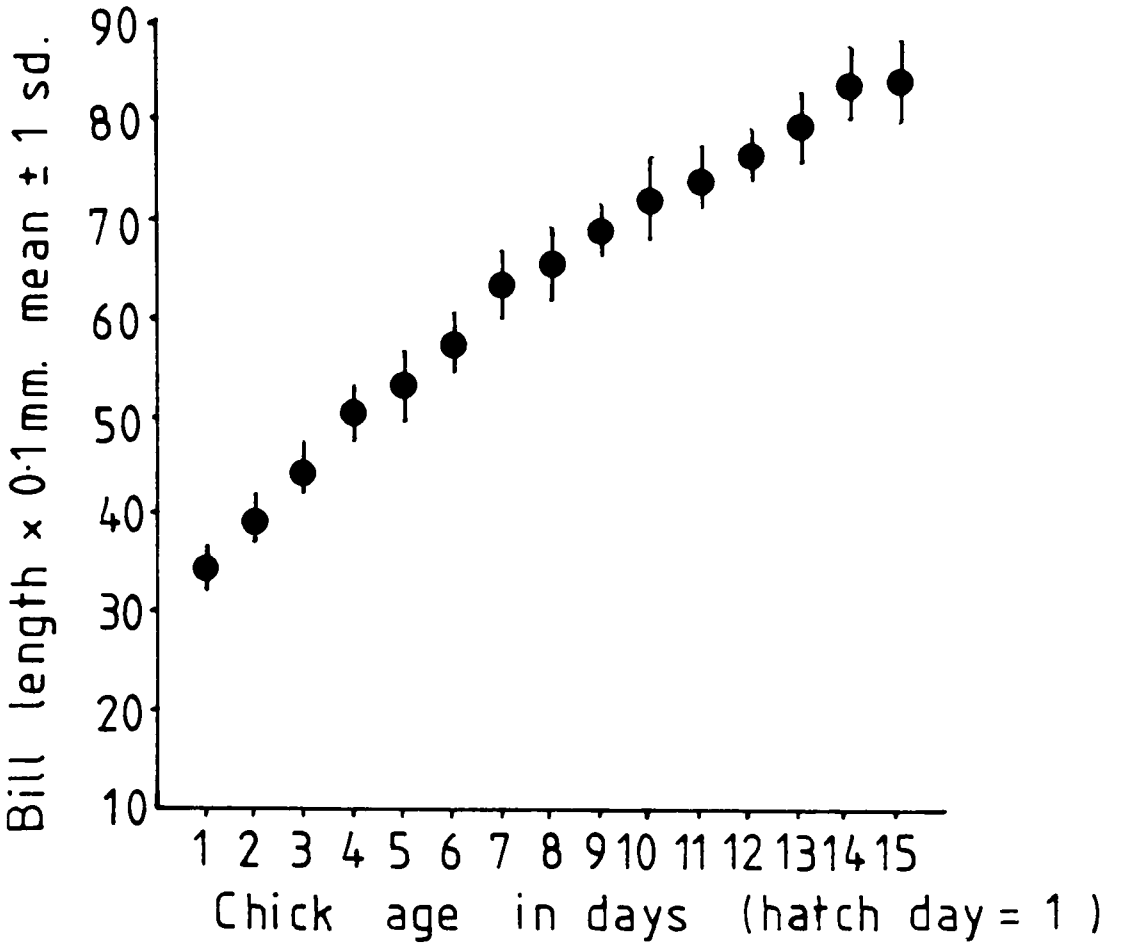


Figure 3.6 The growth in bill length with age in Great tit nestlings measured during the summer of 1985. Sample sizes are given in Table 3.13.

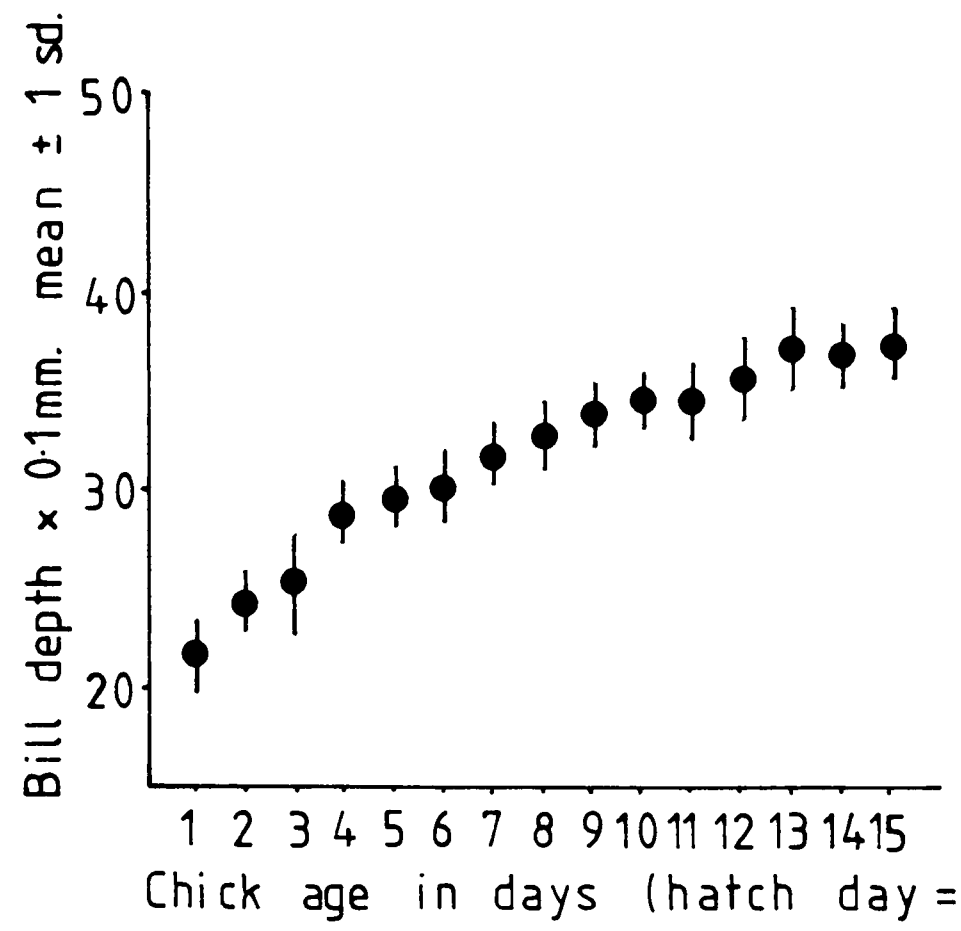


Figure 3.7 The growth in bill depth with age in Great tit nestlings measured during the summer of 1985. Sample sizes are given in Table 3.13.

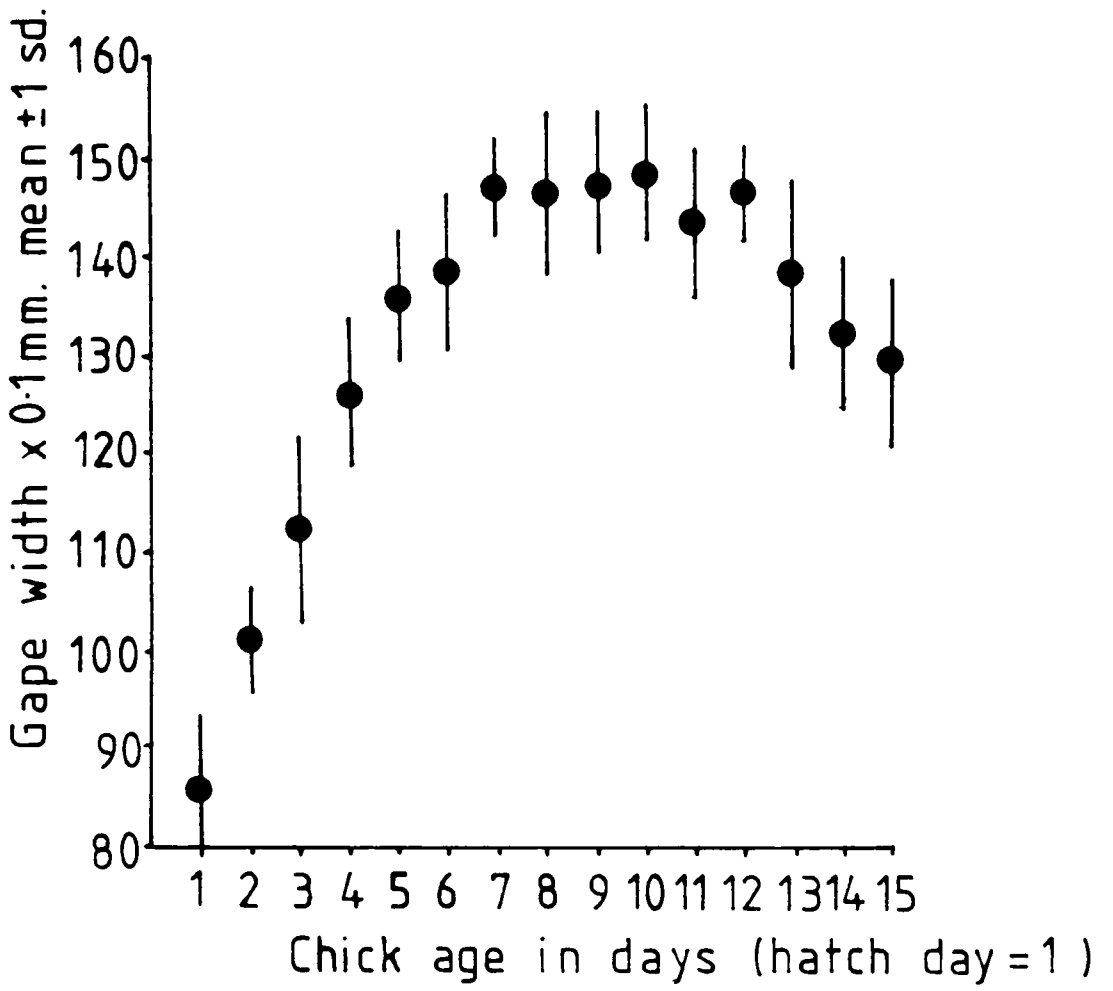


Figure 3.8 The change in gape-flange width with age in Great tit nestlings measured during the summer of 1985. Sample sizes are given in Table 3.13.

nestling take longer to develop (O'Connor 1984). Similarly, growth rates differ amongst the three bill characters indicating their relative importance to the nestling. Hence the gape flange which acts as a target for the feeding parent, increases most rapidly in size to a maximum at about day 7 or 8. This corresponds to an increase in prey size during this period. Royama (1966) found that the size of prey fed to the nestlings increased significantly during the first 7 or 8 days of the chick's life. After this, prey size remained constant. From about day 12 the flange is re-absorbed. The mean rictal width of 17 adults measured in 1986 was 7.0 $\pm$ 0.57mm. Table 3.14 shows the percentage of the full grown dimension reached by 1, 5, 10 and 15 days of age. For bill length and depth the full grown measurement was taken as the mean of data collected in autumn 1985 for the same cohort.

Figure 3.9 shows the change in the coefficient of variation of bill length and bill depth with age of the nestlings. A decline in relative variation occurred in both characters as the nestlings grew older although the trend in bill length was not significant. Since hatchling weight correlates highly with egg weight in the Great tit (Jones 1973), the high relative variation in bill size of very young chicks might reflect the variation in egg weight. To test this I correlated the mean egg weight (of four eggs per clutch) with the mean bill depth for each of the ten broods measured on day 1. The correlation coefficient of 0.053 was not significantly different from 0. Hence it is not clear why a decline in variation should occur with age in this character. Indeed, it may be due in part to measurement error since the bill is very soft and flexible in young nestlings so reducing the accuracy of measurement. Also, in both bill length and depth, the coefficient of variation varies independently of age after about day 6. However it seems unlikely that this could double the observed variation. Such measurement error should not affect

Table 3.14 Bill size in nestlings of different ages expressed as a percentage of the full-grown bill dimension.

AGE (days).	Bill length.	Bill depth.	Gape width.
1	32.5%	51.9%	122.1%
5	49.9%	70.5%	195.1%
10	67.5%	82.6%	211.5%
15	78.7%	89.4%	185.2%

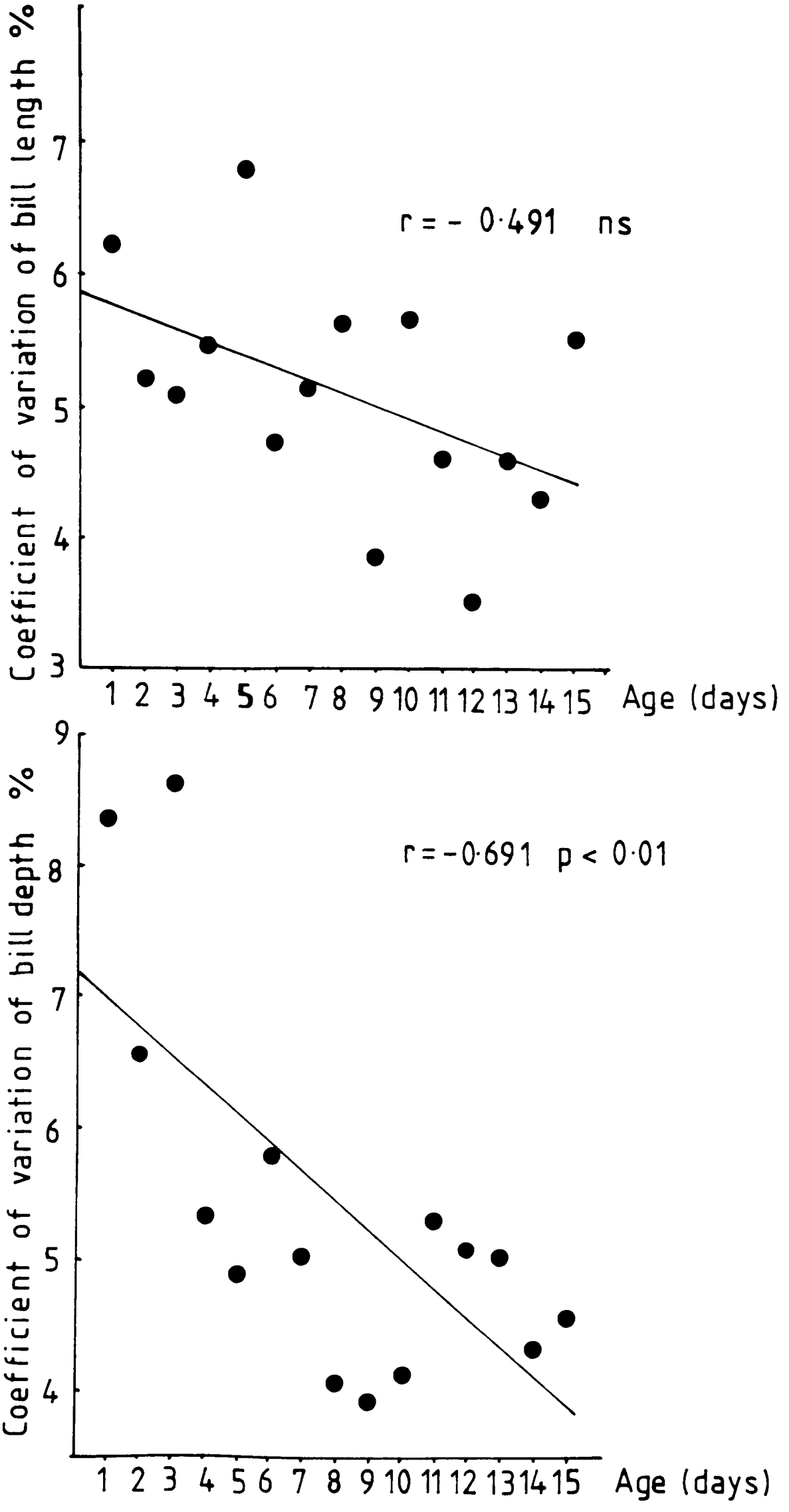


Figure 3.9 The drop in relative variation in bill length (top) and bill depth (bottom) with age in Great tit nestlings measured during the summer of 1985. Sample sizes are given in Table 3.13.

significantly the mean values shown in figures 3.6 and 3.7

3.5.1 Sources of variation in the nestling bill.

In the last section I showed that the coefficient of variation of bill depth in fifteen day old nestlings in 1984 was 4.2% (for bill length measured in 1985 it was 5.5%). This is comparable with figures obtained for the full-grown population (see Table 3.1). This section examines sources of this variation. The following analyses are restricted to bill depth since this is more fully developed at fledging than any other bill character (see Table 3.14 above) and because bill depth is less influenced by the indeterminate growth of the rhamphotheca which causes considerable 'within-bird' variation in bill length (see sections 3.6 and 3.7).

Of the 433 nestlings measured in 1984, 66 were subsequently retrapped and sexed during the following winter. Until the 14th of November they were trapped whilst taking fruit at Elder patch. From then onwards they were trapped whilst feeding on mast (see methods). The mean bill depth of these 66 birds when they were 15 days of age was 3.833 $\pm$ 0.087mm (n=66). This did not differ significantly from the population mean of 3.832 $\pm$ 0.161mm (n=433). A single classification ANOVA was carried out to determine the proportion of variance in the nestling measurements that was due to sex. The ANOVA is presented in Table 3.15. This shows that only 7.25% of the variance in bill depth in this sample was due to sex, although this was significant. However, Table 3.16 shows that 46.9% of the variance in the 'full-grown' measurements of the same birds was due to sex. This result was highly significant.

This difference in the importance of sex as a contributor to bill variation

Table 3.15. Analysis of variance to determine the contribution to variation in bill depth made by sex in 66 nestlings sexed on recapture.

Source of variation.	d.f.	s.s.	m.s.	F.	P
Sex	1	14.732	14.732	5.004	<0.05
Error	64	188.435	2.944		
Total	65	203.167			

Table 3.16. Analysis of variance to determine the contribution to variation in bill depth made by sex in 66 first-year Great tits measured during the winter of 1984/85 and used in Table 3.15.

Source of variation.	d.f	s.s.	m.s.	F.	P
Sex	1	153.15	153.15	56.55	<Ø.ØØ1
Error	64	173.33	2.71		
Total	65	326.48			

between ages is considered further in the next section. Although sex contributed little to the variance in bill depth among nests, within nests it was more important. A single classification ANOVA was carried out to determine the influence of sex on the measurements of the sexed nestlings after expressing each measurement as a deviation from its brood mean. The ANOVA table for this analysis is shown as Table 3.17. This shows that 17.35% of the variance was due to sex when between-nest effects were removed, and this was highly significant. Table 3.18 shows the distribution of bill depth relative to the brood mean. This suggests that most of the sex deviation was caused by a tendency for males to exceed their brood mean. Female measurements were more evenly distributed about the mean.

To analyse further the relative contributions made by a series of environmental and/or genetic factors to nestling bill depth, a stepwise multiple regression analysis was carried out with the 15th day bill depth as the criterion variable and with six predictor variables. The analysis was carried out on brood means of the characters, hence 63 broods were available initially for analysis. However, due to variation in sample sizes for the predictor variables, the final sample size available was 42. The predictor variables used were as follows:

1. Brood size (n=63). The number of chicks in a brood is known to influence the mean fledging weight of chicks by its relationships with food availability to each chick and to thermoregulation (Perrins 1965, Royama 1966, O'Connor 1973).

2. Mean chick Weight (n=63). This gives a relative measure of body size between broods. Chick weights were standardised relative to time of

Table 3.17. Analysis of Variance to determine the contribution made to variation in bill depth within nests.

Source of variation.	d.f	s.s.	m.s.	F.	P
Sex	1	25.95	25.95	13.44	<Ø.ØØ1
Error	64	123.58	1.93		
Total	65	149.53			

Table 3.18. The distribution of bill depth by sex with respect to the brood mean in 66 sexed nestling Great tits.

	male	female
Bill depth > brood mean	34	11
Bill depth = brood mean	3	1
Bill depth < brood mean	5	12

day although chick weights were remarkably constant through the day. Weights were adjusted to 12 noon using the regression equation Wt = 18.34 + 0.044 time. This variable is not independent of brood size or parent weight (which contributes an heritable component), but when these two variables are held constant, the remaining covariance with bill depth is due to covariance with variation in the growth environment. Figure 3.10 shows the relationship between mean chick weight and mean chick bill depth in this sample.

3. Mid-parent mean weight (n=59). This was entered to remove the heritable component of mean chick weight (however, see note below). the slope of the regression of offspring on parent weights gives an heritability estimate of 44.4% for the present sample (see the section on heritability or Falconer 1981). Parent weights were also adjusted to 12 noon using the equation Wt = 18.22 + 0.0528 time.

4. Mid-parent mean bill depth (n=60). This contributes an heritable component to bill depth. Regression of offspring mean on parent mean bill depth gave an heritability estimate of 29.5% for the present sample (see Falconer 1981). This is low when compared with the heritability of the same character in full grown offspring (see section 3.6.2) because the full expression of genetic variation is only achieved when fully-grown. Figure 3.11 shows the relationship between mean parent bill depth and mean chick bill depth in the present sample.

5. Date (n=63). The date on the brood's 15th day, where May 1st = 1. Fledging weight may decline with date through the season due to a change in the

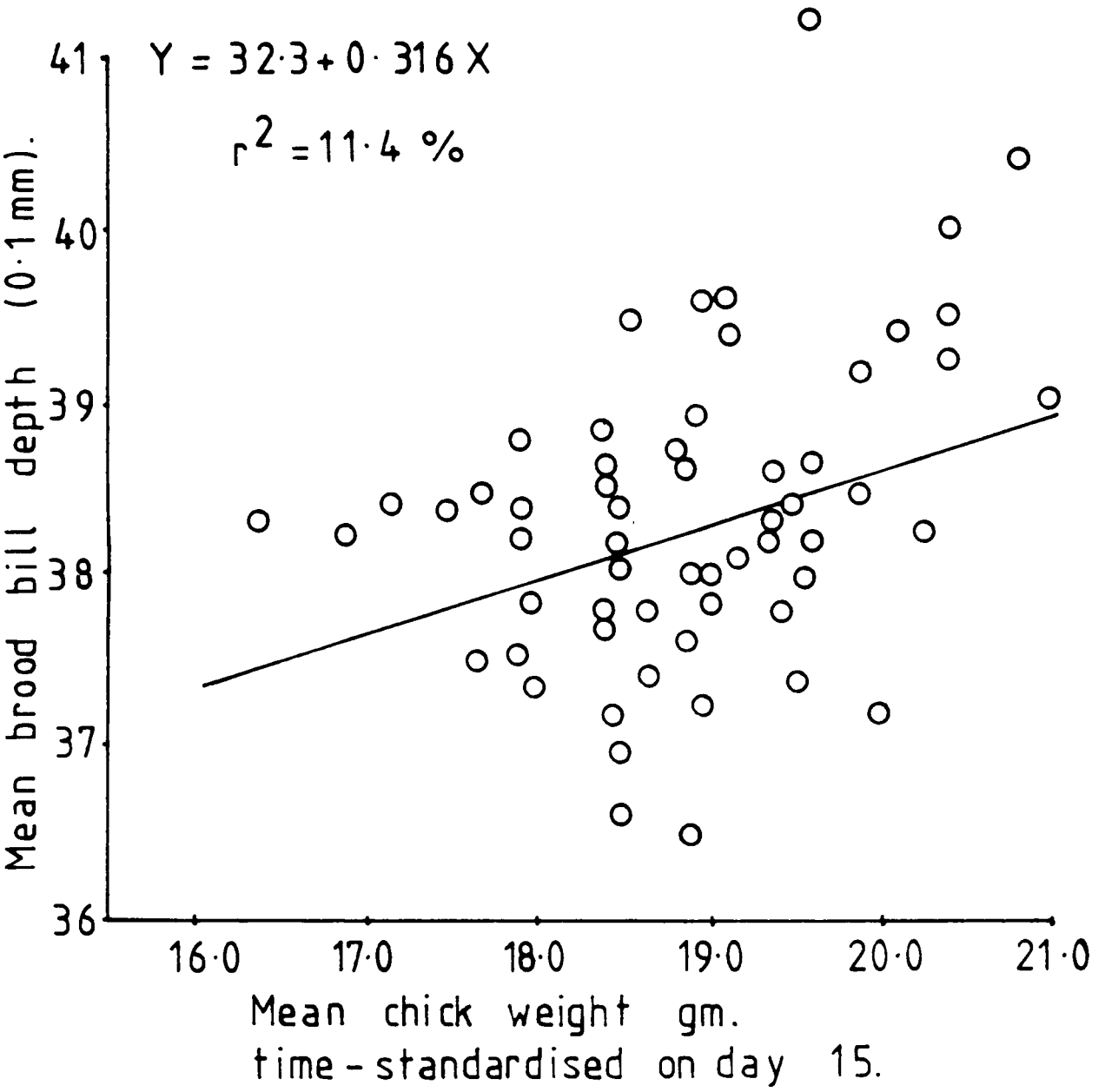


Figure 3.10. The relationship between chick weight - as mean chick weight per brood on the 15th day of life and bill depth - as mean chick bill depth per brood on the same day for 63 broods of Great tits measured during the summer of 1984.

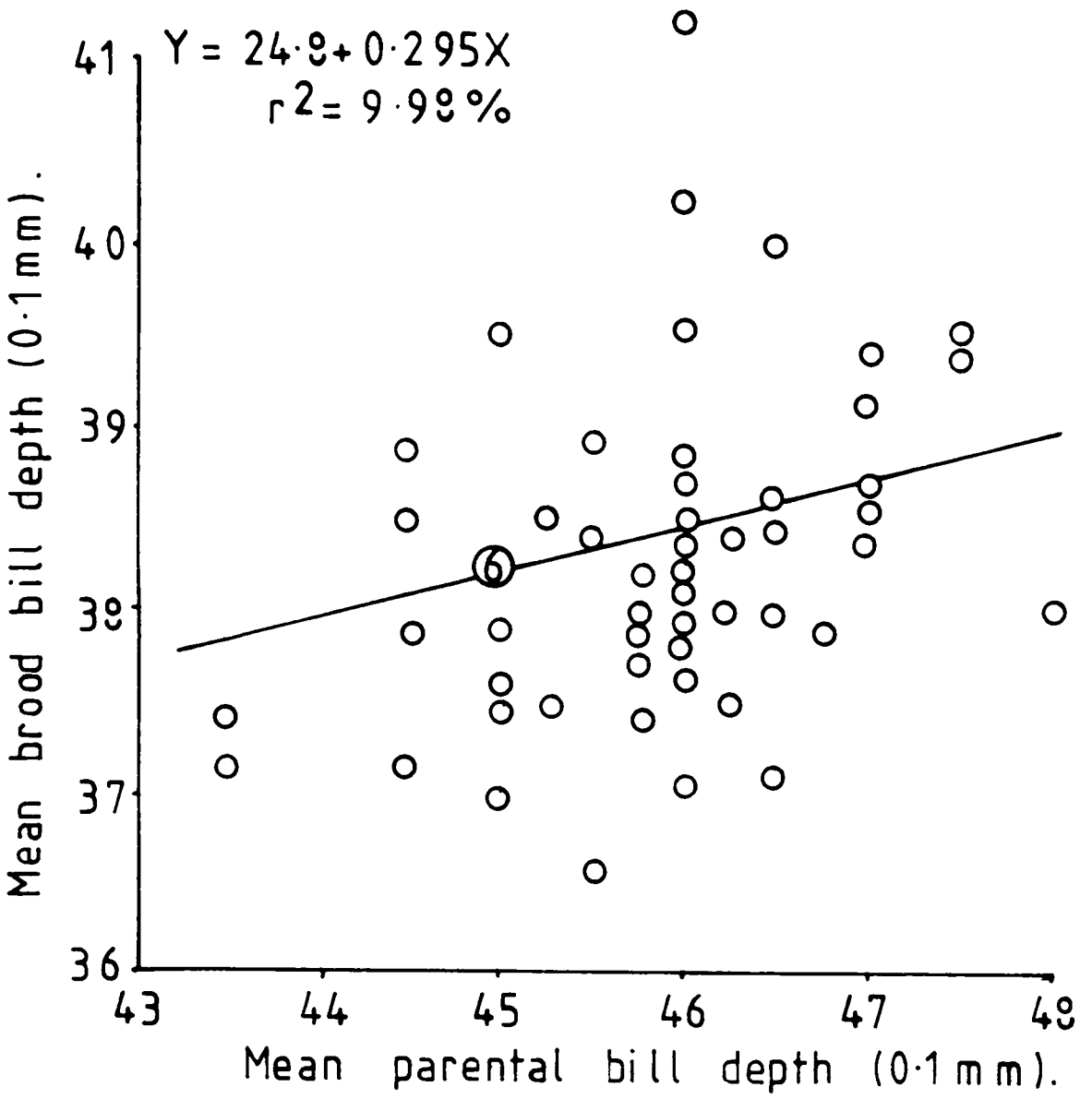


Figure 3.11. The relationship between bill depth in 15 day old nestlings - as a brood mean, and the mid-parent mean bill depth for 63 broods of Great tits measured during the summer of 1984. The relationship was very poor. Note that the regression slope in this case does not indicate the heritability of the character since the bill was not yet full-grown in the nestlings.

quality and/quantity of food available (Perrins 1965, 1976). In the present sample mean chick weight and date were significantly correlated (r_{61}=-0.483, P<0.001).

6. Non-caterpillar prey (NCP) score (n=42). This gives some measure of prey quality assuming that caterpillar prey are preferred, the proportion of non-caterpillar prey gives a measure of caterpillar availability to the parents. The score (0-5 relative to abundance) was obtained by an analysis of chick faecal sacs taken on the 15th day. The scoring method is described fully in chapter 5. A partial correlation analysis showed that the covariance between date and chick weight was largely due to prey quality (NCP). NCP increased significantly with date, and chick weight declined as a consequence. The partial correlation coefficients were $r_{\text{Wt Date.NCP}}$= -0.052 (NS) df=39, and $r_{\text{Wt NCP.Date}}$=-0.425 P<0.01 df=39.

The analysis gives partialised r^2 values for each variable, that is, the percentage of variance in chick bill depth explained by covariance with each predictor when every other was held constant. The results are presented in Table 3.19.

It should be noted that the heritable component of chick bill depth referred to above cannot be removed (or indeed estimated) entirely because of the correlation between parent 'quality' and territory quality (environment). For this, brood manipulation must be carried out. However, with this caveat in mind, Table 3.19 suggests that most of the explained variance is due to variation in the growth environment, either brood size or the environmental component of mean chick weight. Although over half of the

Table 3.19. The proportion of variance in chick bill depth due to covariance with each of six predictors entered in a stepwise multiple regression analysis. The figures given are partialised r^2 values.

Predictor.	Partial r^2.	Significance of partial r.
Chick Wt	18.7%	P<Ø.Ø1
Brood size	12.5%	P<Ø.Ø5
Parent bill depth	6.6% *	NS
NCP	3.4%	NS
Date	Ø.5%	NS
Parent Weight	Ø.5%	NS

* Note: This is not a measure of heritability, but a measure of partial covariance.

variance in bill depth remains unexplained, the growth environment probably contributes the major part since any genetic variation represented by this unexplained component must be uncorrelated with differences in the chick weight or the parent's full-grown bill size.

3.5.2. Post-fledging development of the bill.

Since the bill is fully-grown by the first October of life, the ratio of the nestling bill depth to the winter value gives the proportion of the final bill depth achieved at fledging in the retrapped sample. This was 87.43 $\pm$ 4.56% (n=24) for females and 83.87 $\pm$ 3.75% (n=42) for males. The difference between the two sexes was highly significant (t_{65}=3.247, P<0.01), despite the sexes having diverged little in bill depth by the 15th day of life (Only 7.25% of the variance in bill depth was due to sex as compared to 46.91% in the same sample in the following winter). The little divergence that had occurred by the 15th day is indicated also by a comparison of the coefficients of variation for the whole population at different developmental stages. For winter 1984 the coefficient of variation for the sexes combined was 4.87% comprising 3.59% for males and 3.28% for females. The coefficient of variation for 433 nestlings was 4.19%, ie: between the full grown level of variation and that expected for a nestling population with no sex deviation (suggested by the single sex coefficients).

Although some divergence had occurred by the time that 80-90% of growth in bill depth was complete (at day 15), this was small compared with the final degree of sexual dimorphism, and suggests that females reach a 'plateau' in bill depth earlier than males.

Figure 3.12 shows the relationship between bill depth at 15 days and when full-grown (measured in the first autumn). The correlation coefficients between these measurements are given in Table 3.20. This indicates that at best only 14.98% of the variance in the final bill depth was contributed by the bill variation in the nest and this itself contained a sex-specific

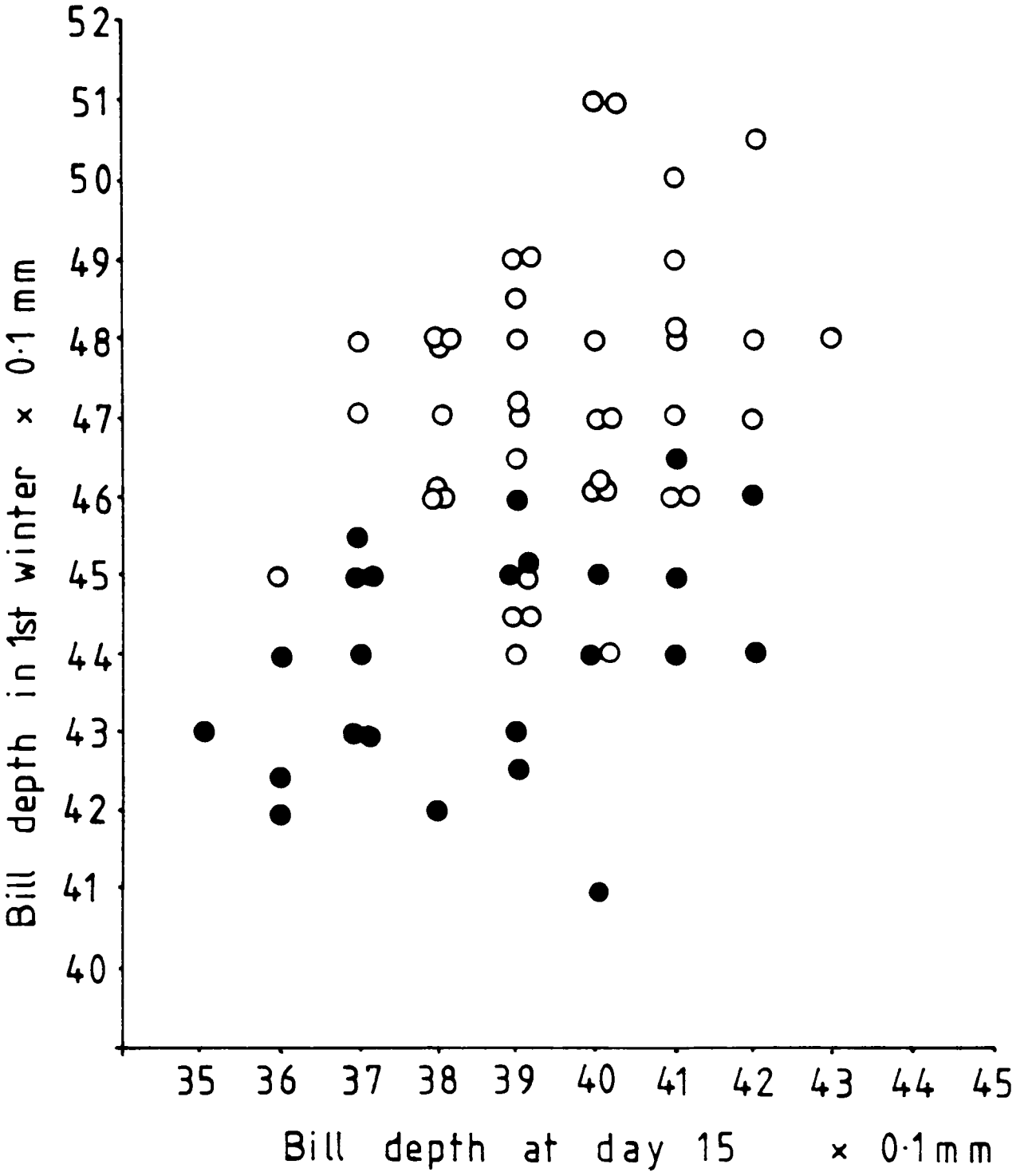


Figure 3.12. The relationship between bill depth in the nest (at 15 days) and on recapture when full-grown during the first winter in 66 retrapped Great tits initiall measured during the summer of 1984. Note: Open circles are males, closed circles are females.

Table 3.2Ø. The correlation between bill depth at 15 days and when full-grown the following winter.

Group.	r.	r^2.	n.	P.
males	Ø.274	7.5Ø%	42	NS
females	Ø.361	13.Ø3%	24	NS
combined	Ø.387	14.98%	66	P<Ø.Ø1

component.

To analyse further the contribution made to the final bill depth by a series of components, a stepwise multiple regression was carried out with the final bill depth as the criterion variable. The following five predictor variables were entered: (1) sex, (2) date of capture in winter (October 1st=1), (3) bill depth at day 15, (4) tarsus length as a measure of body size, (5) site (whether captured whilst feeding on fruit at the Elder patch or on beech mast at the mast sampling sites A1 and A2 see Fig 2.4). Table 3.21 gives the partial r^2 values calculated by this analysis.

Table 3.21 shows that development in the nest played only a small part in determining the final bill depth and the same might be expected of bill length since rather more of its development is completed after fledging (Table 3.14).

In the last section I showed that much of the sex deviation in nestling bill depth was due to a male bias. The mean deviation for the sexed nestling sample was 0.062 ± 0.152mm (n=66). This differed significantly from the mean deviation of the whole population of 0.001 ± 0.145mm (n=433) ($t_{498}=3.068$, $P<0.01$). If winter sampling was unbiassed with respect to bill depth, this suggests that either the nestling population showed a strong bias in sex ratio favouring females, or natural selection favouring deep-billed males had occured between fledging and capture in the autumn. The stepwise multiple regression analysis presented above (Table 3.21) showed that bill depth varied independently of capture site. While this does not prove that sampling was unbiassed, it nevertheless suggests that it was. Dhondt (1970) showed that nestling sex ratio was more or less at unity in the Great tit. Indeed when differential mortality occurred in the nest, it favoured males. Hence it

Table 3.21. The proportion of variance in final bill depth due to covariance with each of five variables entered as predictors in a stepwise multiple regression analysis. The figures given are partialised r^2 values.

Predictor.	Partial r^2.	Significance of partial r.
Sex	46.91%	P<Ø.ØØ1
Date	7.60%	P<Ø.Ø5
Bill depth at day 15	2.91%	NS
Tarsus length	Ø.30%	NS
Site	Ø.Ø1%	NS
Total	57.73%	

seems most likely that the excess of deep-billed male nestlings in the retrapped sample resulted from selection of deep-billed males during the intervening period (ie: between fledging and autumn sampling). It is known that mortality is highest during the three months after fledging and that selection favours heavier individuals (Perrins 1965, Perrins and Dhondt in prep.) Since the greatest component of nestling bill depth was explained by its covariance with body weight, it is possible that selection for weight in male fledglings led to selection of bill depth (for terminology see Endler 1986). Since males are heavier than females the lack of such a relationship in females could arise if the mean body weight of female fledglings were below a threshold of weight-mediated survivorship, that is, if weight and survival were related by a positively accelerating curve so that a large increase in weight within the female weight range had little effect on survival, but a relatively small increase in weight within the male weight range greatly increases the prospect of survival. I shall return to this subject again in chapter 7 on natural selection where I shall present strong evidence that selection acts differentially on bill characters in the two sexes during the first three months of life.

3.6. Seasonal variation, repeatability and heritability.

3.6.1 Seasonal variation in bill characters.

Few studies have looked in detail at seasonal variation in bird morphology. In studies of the Great tit, most have worked either with hard morphological characters such as tarsus length which are fully grown at or shortly after fledging and which change little during life (Garnett 1981), or with traits such as clutch size in which seasonal effects are readily examined and/or controlled.

The histology and development of the rhamphotheca is directly comparable with that of the foot papillae which show seasonal changes in thickness (Lennestedt 1975). Despite a long recognition that the structure of the rhamphotheca endowed it with great potential for rapid change (Newton & Gadow 1896, Ludicke 1933), both taxonomists and ecologists have assumed that bill size was fixed during the life of the individual. Ludicke (1933) found that in the Canary Serinus canaria the growth rate of the rhamphotheca at its tip was 0.076 mm day^{-1}. Rhamphothecal cells (initiated by a basal epithelium) migrated to the surface of the tissue in such a manner that growth in both bill length and depth was possible. Further, growth rate was a function of the rate of wear at the tip and tomia. This physiological feedback between the rates of keratin loss and production has since been shown in the Human finger nail (Hillman 1955), and in the Oystercatcher bill (Hulscher 1985). Ludicke (1933) also reported growth rates of 0.38 mm day^{-1} in the Great-spotted Woodpecker bill and 0.05 mm day^{-1} in the pigeon Columba livia bill. Wydoski (1964) found a growth rate of 0.07 mm day^{-1} in the Starling bill, and Hulscher (1985) reports a growth rate of 0.44 mm day^{-1} in the Oystercatcher bill. These measurements

were all made over periods of several weeks. In the present study, such growth rates would show significant changes in bill length in only a few days (measurement to 0.1 mm).

Several taxonomists have stressed the importance of seasonal variation in bill length (Clancey 1948, Marshall 1948, Davis 1954, Davis 1961, Packard 1967 and Johnson 1977), but their studies were based on museum specimens and have made rather little impact. Selander (1958) found that seasonal variation in the bill of the Boat-tailed Grackle Quiscalus major was so great that it could not be ignored in studies of geographical variation in the species. Few studies have been carried out on live birds. Green (1981) found that bill length in the Rook Corvus frugilegus decreased within known individuals through the summer due to increased abrasion while probing into ground which became harder through the summer.

Most of the studies cited above concern granivorous (or principally so) or passerine species which switch to an insect diet in summer. All show the same pattern of increased bill length in summer, declining again in winter. It is generally believed that this results from the reduced bill abrasion of the food when the birds switch to the softer invertebrate diet. In the Great tit, Ludescher (1968) showed that when hammering seeds, only the tip of the upper mandible made contact with the seed. Hence, seasonal changes due to differences in food hardness should be more apparent in bill length than depth in this species. Van Noordwijk & Klerks (1983) suggested that seasonal variation in bill length must occur in the Great tit as they obtained higher estimates of heritability than repeatability. Falconer (1981) pointed out that repeatability must set an upper limit to estimates of heritability. Similarly in the present study, the difference between long and short-term repeatability in bill characters presented in Table 2.4 suggests that a

seasonal component of variation exists.

Figure 3.13 shows mean monthly values (± 1 s.e.) for the three bill characters during the study period. Only Wytham-hatched birds were used in this figure, but all age classes were included. Significant seasonal effects were observed in all characters but only bill length showed a clear and dramatic seasonality, being longer in summer than in winter (as described in other species). Figure 3.14 shows the relationship between changes in the mean bill index of males and females between seasons in the whole population and changes within individuals measured in both seasons. The correlation between these variables was very high (r_{10}=0.938, P<0.001), indicating that changes between seasons in the population as a whole were due to changes within individuals and not to seasonal bias in trapping.

Figure 3.13 suggests that most of the seasonal variation in bill index was due to changes in bill length. However, in all three cases, the mean bill depth of males measured in both seasons increased from summer to winter, but decreased from winter to summer. No such pattern (nor significant change) was observed in females. Further, males re-measured during the winter of 1983/84 (feeding on mast) had significantly deeper bills than in the previous summer (t_{70}=2.706, P<0.01). Figure 3.15 shows changes in bill index of known individuals during the winter of 1983/84. This supports further the proposition that seasonal changes in the mean of the population were due to changes within individuals. Since the pattern of seasonal change in bill depth was not observed in females it is unlikely that this was due to a seasonal change in the measurement criteria. Hence there is some evidence for an increase in bill depth in males in winter.

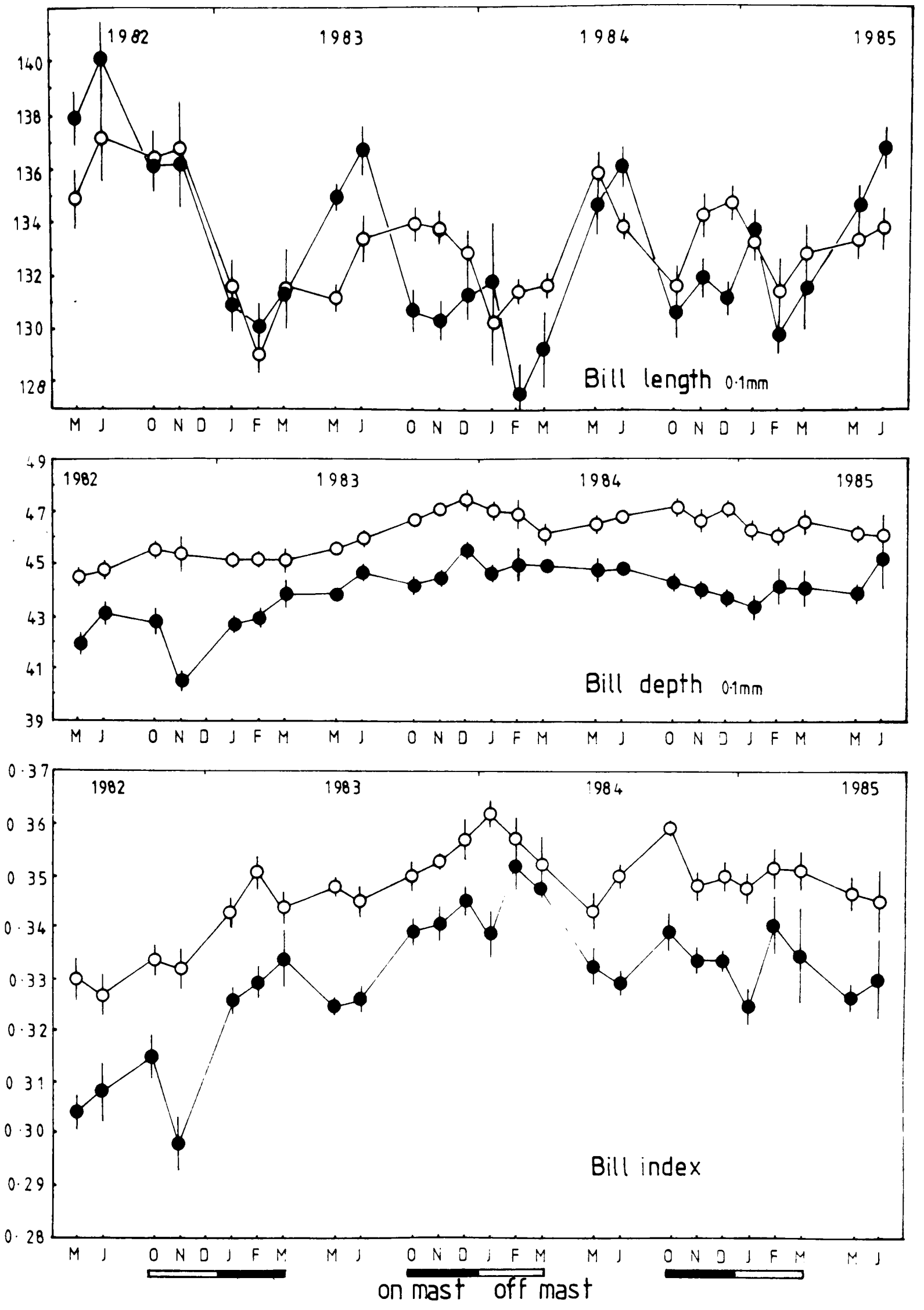


Figure 3.13. Bill changes in the Wytham resident population between May 1982 and June 1985. Graphs show the mean ± 1 s.e. of bill length, depth and index in each month of the study for males (open circles) and females (closed circles) for Wytham-hatched Great tits of all ages.

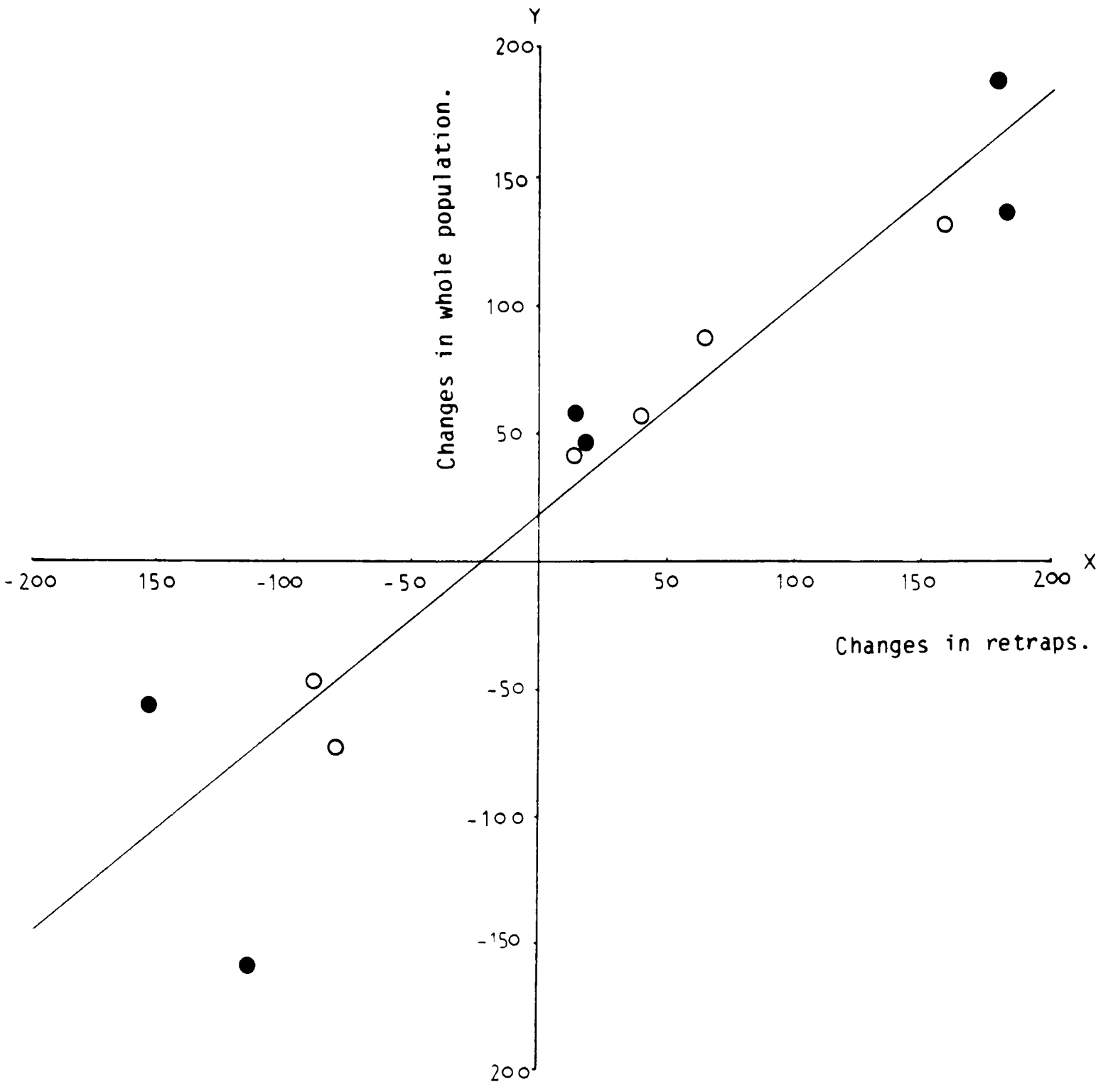


Figure 3.14. The relationship between the mean change in bill index across consecutive seasons of retrapped individuals (x axis) and changes in the mean bill index of the whole population across the same seasons (y axis). Mean differences have been multiplie by 10,000. Changes in males are shown by open circles, females by closed circles. The regression line (Y=18.5+0.831X) was highly significant ($r=0.938, P<0.001$) indicating that changes in the mean of the whole population were due to changes within individuals.

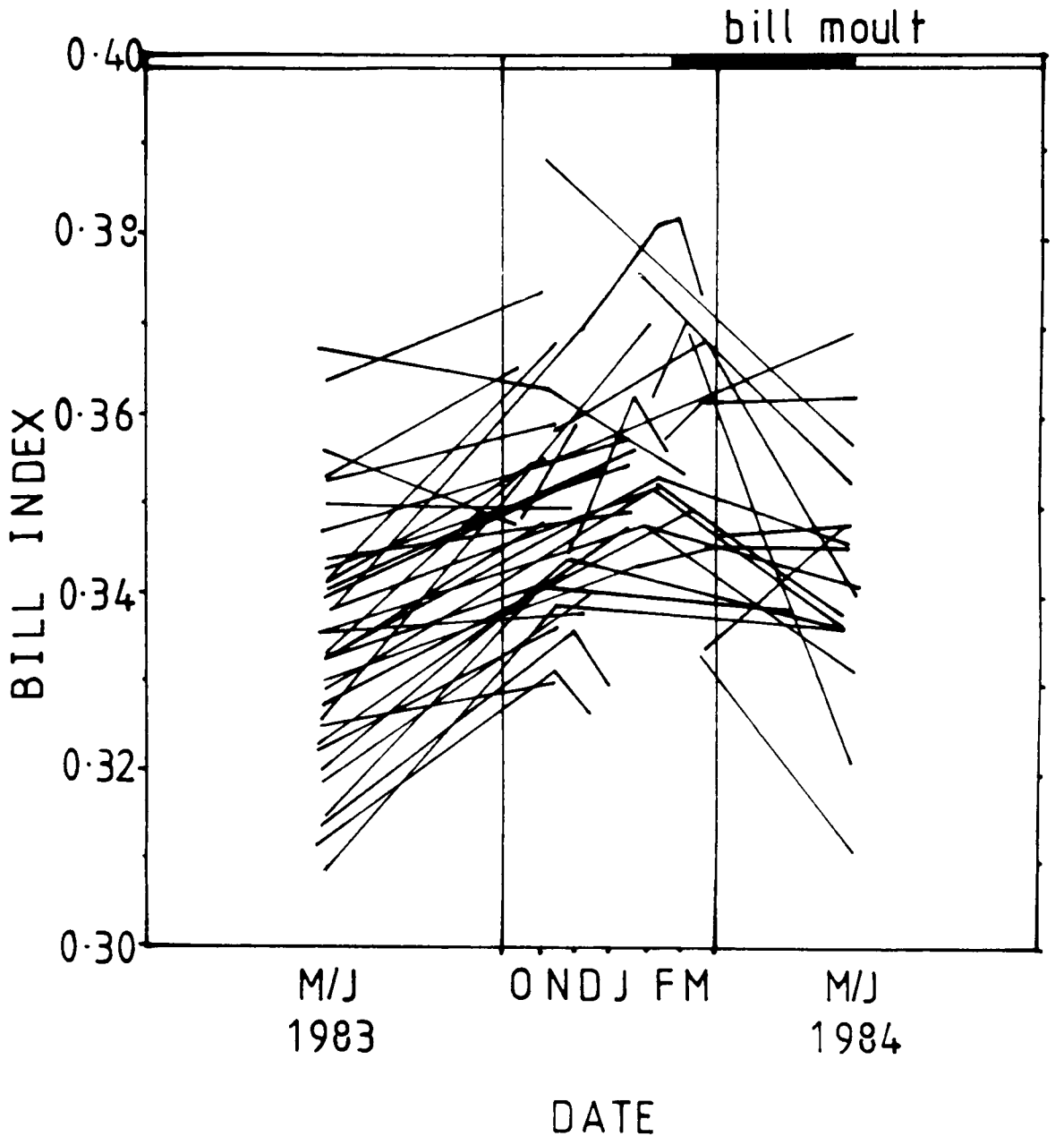


Figure 3.15. Changes in bill index of marked individuals retrapped during the winter of 1983/84. The lines join bill index measurements of the same individual at different times. The figure shows a marked increase in index from the summer of 1983 to the winter which was significant (see text) and a suggestion of a decline following the winter. The period marked 'bill moult' will be considered later.

3.6.2 Repeatability and heritability of bill characters.

3.6.2a Repeatability.

A high repeatability of measurements with time is essential for studies of heritability in natural populations since it is often necessary to measure individuals in different seasons. The method for calculating repeatability was described in chapter 2 (see also Falconer 1981). A genetic (heritable) component of phenotypic variation is essential for natural selection to operate adaptively.

Repeatability measures the change within individuals over time. When a comparison can be made with a standard or 'expected' repeatability determined from measurement error, its significance may also be determined. I have taken the short-term repeatability (within 14 days) described in chapter 2 as a measure of this observer error. Short-term repeatabilities are shown in Table 2.4. One-way ANOVA was used to obtain a measure of within- versus between-bird variation over two seasons for each character. The error mean square (EMS) term, expressing the average within-bird variation, was then used to compare the variation between seasons with the EMS expected from observer error alone. Hence the EMS of birds measured in both summer and the following winter, and in consecutive summers (ie: re-measured after six and twelve months respectively) were compared with the fourteen-day standard in a series of ANOVAs. Repeat measurements of individuals taken within a season were averaged as described in chapter 2. The ratio of long-term (six or twelve month) EMS / fourteen-day EMS determines the significance of long-term variation within individuals relative to the expected value due to measurement error. Further, the ratio of six-month to twelve-month EMS

determines the significance of variation among seasons. Sexes were pooled in these analyses and the results are shown in Table 3.22.

Table 3.22a shows that variation within individuals between summers was significantly greater in all characters than expected from measurement error. Table 3.22b shows that in most cases variation was as great between summer and winter as between summers, but in four cases out of nine (Table 3.22bii) there was significantly more variation between summer and winter (ie: after six months) than between summers (ie: after twelve months). The reverse situation (ie: twelve-month variation greater than six-month) was never statistically significant. Since all birds used in this analysis were breeding (and therefore at least one year old) when first used in the analysis, age differences were not responsible for these results. Hence bill characters tend to become more variable in winter than in summer. Insufficient data were available to make similar comparisons between winters.

Table 3.23 shows the coefficient of determination (r^2) between measurements of individuals across seasons. Repeat measurements of individuals made within a season were averaged for that season (as described in chapter 2). Note that in every case the coefficient of determination of bill length was higher between summers (12 months) than between the appropriate summer and winter (6 months), indicating a cyclical return to the summer value. This was not true of bill depth. Note also that in general, more variance was explained in bill depth than in bill length in winter. Further, in the winter of 1982/83 bill length in both sexes showed an extremely low correlation with (dependence on) that in the previous summer, and may have been effectively independent of it. This was not true of bill depth in that season.

Table 3.22 The comparison of error mean square (EMS) of bill characters for birds measured in successive seasons.

a) Comparison of birds retrapped between summers. F ratios are shown for 12 month/14 day EMS together with levels of probability. Numerator degrees of freedom are given. Denominator degrees of freedom are 113 throughout.

		F RATIO		
Season	d.f.	Bill length	Bill depth	Bill index
Su82-Su83	47	6.65 ***	4.78 ***	6.24 ***
Su83-Su84	46	3.31 ***	3.88 ***	3.16 ***
Su84-Su85	56	2.Ø6 **	2.25 **	1.72 *

b) Comparison of birds between summer and winter. (i) compared with 14 day EMS. (ii) compared with the appropriate 12 month (summer to summer) EMS. Error degrees of freedom are given for the numerator. Degree of freedom for the denominator is 113 for part (i) and for part (ii) is as given in (a) above.

		(i) F ratios			(ii) F ratios		
Season	d.f.	B.L.	B.D.	B.I.	B.L.	B.D.	B.I.
Su82-Wi82/3	2Ø	16.3Ø***	3.63*	18.31***	2.46**	ns	9.13***
Su83-Wi83/4	43	6.97***	3.9Ø***	4.41***	2.11**	ns	ns
Su84-Wi84/5	19	5.85***	2.2Ø*	ns	2.84**	ns	ns

Table 3.23 r^2 values fore comparisons within individuals between seasons. Most correlations were highly significant.

Season	Character	Male	n	Female	n	All	n
Su82-Wi82/3	Bill length	7.7%	13	Ø.3%	8	13.6%	21
	Bill depth	78.8%	13	46.2%	8	65.6%	21
	Bill index	42.3%	13	26.6%	8	5Ø.4%	21
Su82-Su83	Bill length	6Ø.7%	23	33.3%	25	47.3%	48
	Bill depth	66.1%	23	48.9%	25	58.8%	48
	Bill index	58.5%	23	45.2%	25	63.8%	48
Su83-Wi83/4	Bill length	32.8%	19	28.6%	24	11.1%	43
	Bill depth	31.Ø%	19	43.Ø%	24	42.3%	43
	Bill index	23.3%	19	42.8%	24	46.1%	43
Su83-Su84	Bill length	44.9%	2Ø	3Ø.Ø%	26	41.Ø%	46
	Bill depth	58.1%	21	35.2%	26	61.2%	47
	Bill index	1Ø.4%	2Ø	3Ø.Ø%	26	45.2%	46
Su84-Wi84/5	Bill length	46.1%	9	59.3%	1Ø	34.8%	19
	Bill depth	59.9%	9	57.2%	1Ø	75.7%	19
	Bill index	8.5%	9	37.7%	1Ø	52.9%	19
Su84-Su85	Bill length	48.3%	25	65.3%	31	59.6%	56
	Bill depth	43.3%	25	45.2%	31	6Ø.2%	56
	Bill index	49.1%	25	57.9%	31	49.6%	56

The greater dependence of summer bill size on the previous summer than the previous winter suggests the presence of a season-specific factor operating more strongly in summer than in winter. Either the influence of environment on bill size is less varied in summer, or there is a genetic component of determination which is more fully expressed in summer.

3.6.2b Heritability.

Heritability in the narrow sense (h^2) is the proportion of phenotypic variation (Vp) that is additive genetic, or Va/Vp. It may be estimated by linear regression of offspring values on mid-parent mean values when both are at an equivalent stage of development. The heritability is then given by the slope of the regression line (Falconer 1981). The precise determination of heritability in natural populations is fraught with pitfalls. Seasonal, age and sex-specific variation may bias the estimate and as Falconer (1981) points out "Standard errors of heritability estimates are uncomfortably large unless the regression or correlation is based on very large numbers,...". The standard error of h^2 is given by the standard deviation of the regression line which is approximately $\sqrt{2}/n$ (Falconer 1981). Attempts should therefore be made to identify and control sources of error. When this is done, the estimate is often sufficient only to determine whether the character shows 'high' or 'low' heritability and for comparing heritability estimates of similarly standardised data. The definition of heritability implies that an estimate of the percentage of phenotypic variation that is environmental in origin is given by $1-h^2$.

The regression method has been used widely to estimate h^2 of a range of characters in wild passerine populations from laying date, egg size (Van

Noordwijk et al. 1980; Ojanen et al. 1979) and clutch size (Perrins & Jones 1974) to body size (Garnett 1976, 1981; Van Noordwijk et al. 1980), various components of body size (Boag & Grant 1978; Grant 1983; and Boag 1983) and dispersal (Greenwood et al. 1979, but see Van Noordwijk (1984) for a critique of its use in this context). A detailed description of the method was given by Falconer (1981) and Van Noordwijk (1980).

To estimate heritability, offspring measurements were first adjusted for sex differences as described by Smith and Zach (1979). In all cases, the parental measurements used were those taken in the summer of the year of hatching of those offspring used in the parent/offspring regression. Heritabilities were then calculated for offspring measured in the following summer (at one year of age) and in the first winter (at four to nine months of age). An attempt has been made to adjust data for this seasonal difference between parents and offspring. The regression equations derived in the preparation of table 3.23 above were used to standardise parent values between summers. This is valid because the period over which measurements were taken within a season was short (2-3 weeks) relative to the period for which the standardisation was made (12 months). Hence in making the adjustment, little of the removed variance was within-season variance. Since in winter the trapping period was long (6 months) relative to the standardisation period (9 months), a similar standardisation for winter would remove variance from within the trapping period itself. This variance is itself a part of the environmental variance being estimated (as $1-h^2$), hence this was not attempted for the winter season. This difference in procedure should be borne in mind when comparing heritability estimates between seasons.

Use of the seasonal correction assumes that parents surviving to be re-

measured in the second summer were a random sample (with respect to the character analysed) of parents that bred in the previous summer. The validity of this assumption is discussed in chapter 7 which deals with the evidence for natural selection of and for bill characters. Both mid-parent mean and offspring measurements were normally distributed. Heritability estimates were obtained by regression of offspring on mid-parent mean values. Regressions were carried out on offspring measured in the winter after hatching, and in the first breeding season after hatching (ie: when approximately 6 and 12 months old respectively). The difference between the seasonally adjusted and non-adjusted h^2 values gives an estimate of the environmental deviation that is due to differences between years.

Table 3.24 shows h^2 estimates $\pm$ 1 s.e. for breeding and wintering offspring for each character in each year of the study. In the first two years heritability estimates for all characters were significantly greater in summer than in winter. In the third year, two characters showed no effect of season on heritability estimates while bill depth showed greater heritability estimates in winter than in summer. Although winter heritability estimates were calculated without a between-season correction for parents, these results together with those for repeatability indicate a strong influence of environment on the winter bill dimensions. It may also suggest that bill variation in summer more closely expresses bill variation that is genetically determined. This was also suggested by a stronger correlation between bill length and depth within sexes in summer, so reflecting skeletal variation. The mean heritability values reported above are comparable with those described by Van Noordwijk and Klerks (1983).

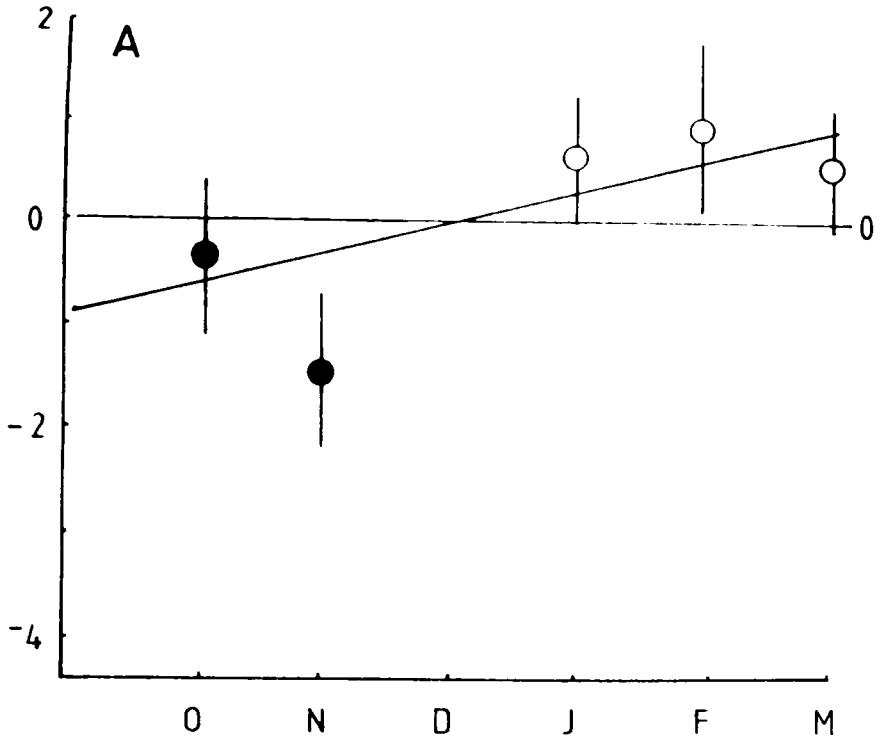
To examine further the environmental component of winter bill variation, I

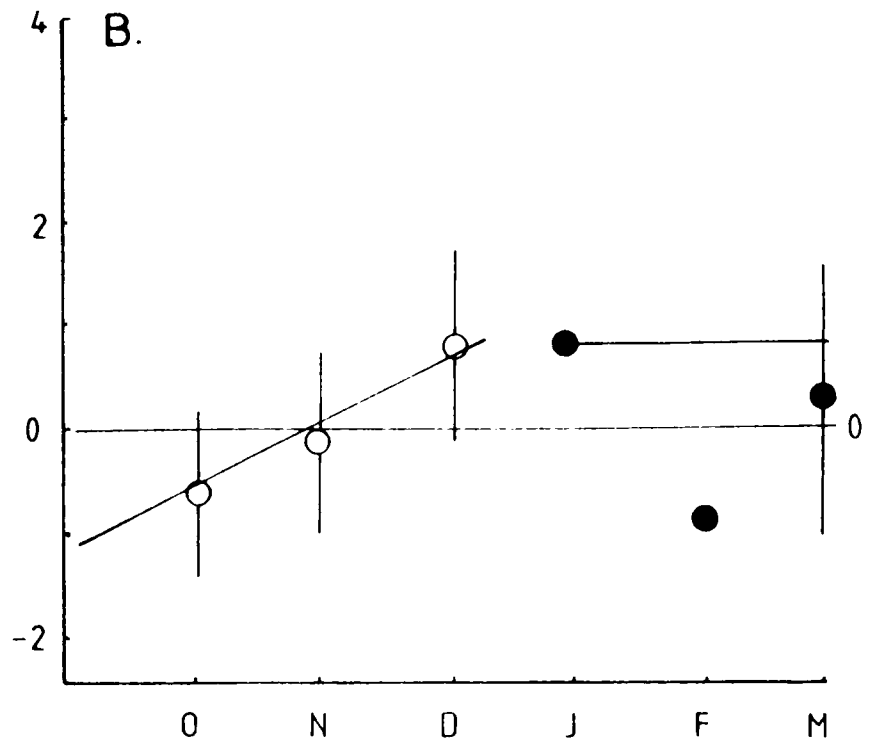
Table 3.24 Estimated h^2 values for all bill characters and seasons with comparisons between summer and winter estimates. In each case, parent measurements were taken in the natal year of their offspring. t values are for comparisons between summer and winter h^2 estimates. All offspring plots were bivariate normal.

		Summer			Winter				
hatch year	char.	n	$\%h^2 \pm 1$se.	E*	n	$\%h^2 \pm 1$se.	t	df	P
1982	Bl	30	60.0±16.7	8.7	69	30.9±18.9	7.64	97	<0.001
	Bd	30	55.8±11.6	5.5	69	26.3±12.4	11.35	97	<0.001
	Bi	30	57.6±17.9	27.9	69	3.8±16.9	10.55	97	<0.001
1983	Bl	46	62.0±31.5	19.2	36	39.7±19.9	3.91	80	<0.001
	Bd	46	56.1±13.5	13.1	36	19.3±25.5	7.85	80	<0.001
	Bi	46	84.1±21.1	27.6	36	49.9±22.7	7.59	80	<0.001
1984	Bl	21	54.5±49.3	14.6	107	37.1±9.7	1.61	126	NS
	Bd	21	7.4±63.5	0.1	107	43.5±16.6	-2.59	126	<0.01
	Bi	21	50.5±39.7	14.5	107	59.4±14.7	-1.01	126	NS

* E=The % environmental deviation due to between-summer effects.

plotted the residuals about the parent/offspring regressions for each character in each winter against the date in winter when the offspring were measured. Figure 3.16 shows these residual plots for bill index in each winter. In two years the birds tended to deviate positively most when trapped at beech sites, suggesting that bill size changed during the winter in response to food hardness. During the winter of 1982/83, bill length became significantly shorter when the birds moved into the beech area. Capture date accounted for 37% of the environmental residual in bill length in that season. Since most of the increase in bill index was due to a decrease in bill length, this was probably caused by increased abrasion at the bill tip. During the winter 1983/84, most captures available to this analysis were made in Brogden's Belt in autumn. Here a significant increase in bill index occurred with date due to a reduction in bill length and an increase in bill depth (see also Figure 3.15). Changes in these components were themselves not significant. However, when combined as a ratio, the opposition of signs gave a significant increase in bill index. In the winter 1984/85, a significant reduction in bill index occurred. Both the highest positive deviation and the highest winter bill index values occurred in October when most birds were caught while taking soft fruit and invertebrates at the Elder patch site. This observation is inexplicable in terms of food hardness. However, the observed change in bill index in each season occurred relative to a standard reference point measured in another season (that is the parent's bill size in the summer). This suggests that changes occurred within individuals and were not produced by sampling bias or selection. The importance of within-winter changes will be discussed further in chapter 4.





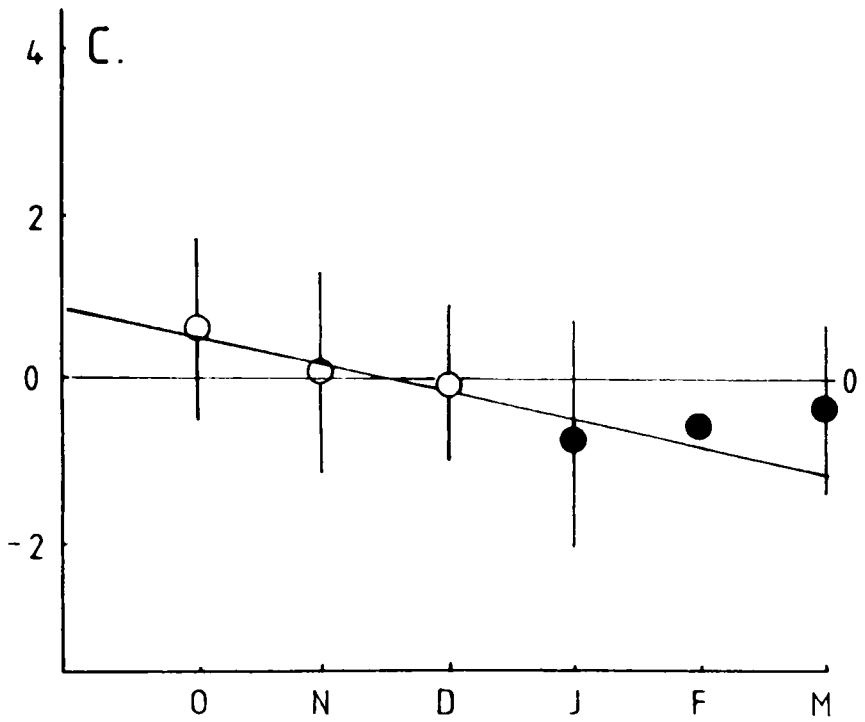


Figure 3.16. The relationship between the residual variation about offspring/parent regression lines (Y) and the date of capture of the offspring in winter (X) during the three winters: A. 1982/83, B. 1983/84, C. 1984/85. Mean residuals $\pm$ 1 s.d. are given for each month. Periods when the birds fed predominantly on beechmast are shown as open circles, closed circles indicate periods when the birds fed elsewhere. The following regression lines were fitted: Fig 3.16A $Y=-0.94+0.293X$, $r=0.553$, $P<0.001$, $n=68$ for the whole winter. Fig 3.16B $Y=1.10+0.54X$, $r=0.390$, $P<0.05$, $n=27$ for autumn. In spring there was no significant relationship ($n=9$). Fig 3.16C $Y=0.664-0.304X$, $r=-0.363$, $P<0.001$, $n=107$ for the whole winter.

3.7 The mode of change of bill dimensions between seasons.

It has long been known that the passerine rhamphotheca grows continuously (Newton & Gadow 1896, Ludicke 1933, Rawles 1960). In this respect it has been compared with the human finger nail (Hulscher 1985). This analogy is useful in considering rates of growth. Hillman (1955) found that nail growth rates were significantly greater in human subjects who bit their nails than in those that did not. Similarly, Ludicke (1933) had shown that in several bird species the growth rate was dependent upon the rate of wear. Hence compensatory cell production/keratinisation occurred, somehow stimulated by physical attrition of the dead tissue of the rhamphotheca. Ludicke also showed that although cell production in passerines occurred over most of the bill 'surface', growth was itself unevenly distributed. Hence cells produced by the basal epithelium were channelled towards the tip and tomia of the bill. The pattern of cell production and migration so described makes possible an increase in both bill length and depth by the addition of tissue to the tip, tomia and culmen. Frenkel and Gillespie (1979) found no variation in the chemistry of bill keratin among conspecifics across a range of species. Hence differences in wear rates among conspecifics are probably not due to differences in the hardness of the keratin.

To examine the relationships between bill index, shape and wear, the close-up photographs described in chapter 2 were used. Photographs of 32 individuals taken during the winter of 1983/84 were available for examination. These birds ranged in bill index from 0.32 to 0.39. The photographic negatives were examined under a low power microscope fitted with an eye-piece graticule. The graticule was then aligned as a tangent to the proximal edge of the culmen as shown in figure 3.17. An index of curvature was

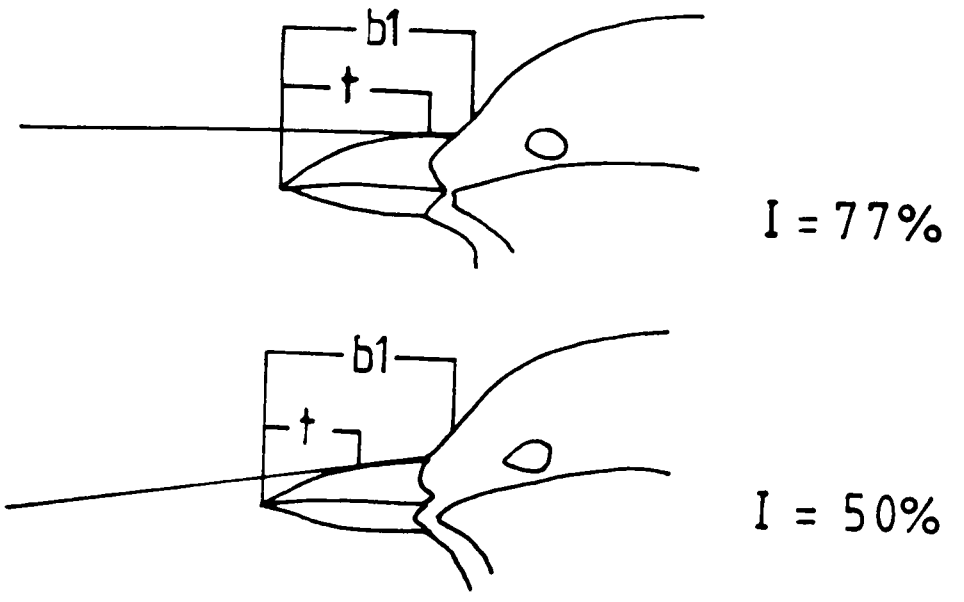


Figure 3.17. Diagram showing the method for estimating the curvature of the culmen from photographs. A tangent is placed on the bill from the base of the bill. The ratio of the distance (t) from the distal point of contact to the bill tip to the total bill length (bl - measured in the field) gives the % of the culmen that is curved. Two examples are shown.

then defined as the ratio of the distance from the bill tip to the point of contact of this tangent to the bill length measured in the field. Figure 3.18 shows the relationship between culmen curvature and bill index. Relatively deep bills tended to have a more rounded culmen. The correlation between bill length and the index of curvature was -0.112 (NS), that with bill depth was 0.419 ($P<0.05$), indicating that bill depth was the principal cause of this relationship.

The same negatives were used to determine the relationship between bill index and wear on the culmen. Culmen wear appeared clearly on the negatives as white scars. Three levels of wear were recognised as:

0 no wear

1 moderate wear

2 heavy scarring

Two photographs were selected as representing scores 0 and 2 and these are shown in Plate 2. These were set aside as standards and excluded from further analysis. An independent observer was then asked to score each photograph using this scale. She was not told the purpose of the experiment and knew nothing of the birds presented. Figure 3.19 shows the distribution of bill index with respect to these wear scores. The difference in bill index among scores were significant. Hence in winter both the curvature and the degree of wear on the culmen increase with bill index. Table 3.25 shows the correlations among these characters for males and females separately. When repeated in summer, all birds showed either a score of 0 or were in bill moult (see below).

Due to the variance in wear scores in the female sample, no covariance was observed between wear and bill characters in females. Hence some covariance between wear and bill index is attributable to sex differences. The longer, thinner bills of females were straighter and received less wear to the culmen

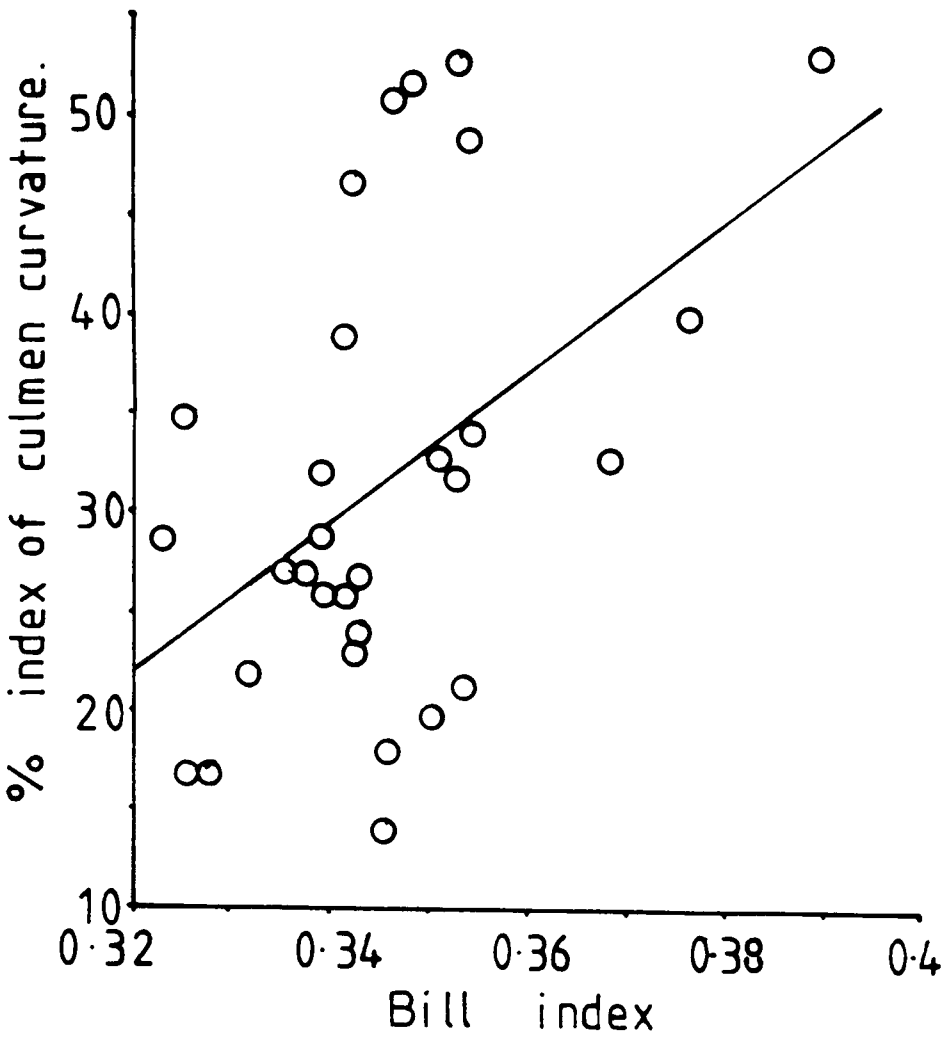


Figure 3.18. The relationship between the index of curvature shown in figure 3.17 and the bill index for 30 photographed Great tits. The regression line Y=-101+385X was significant (r=0.43).

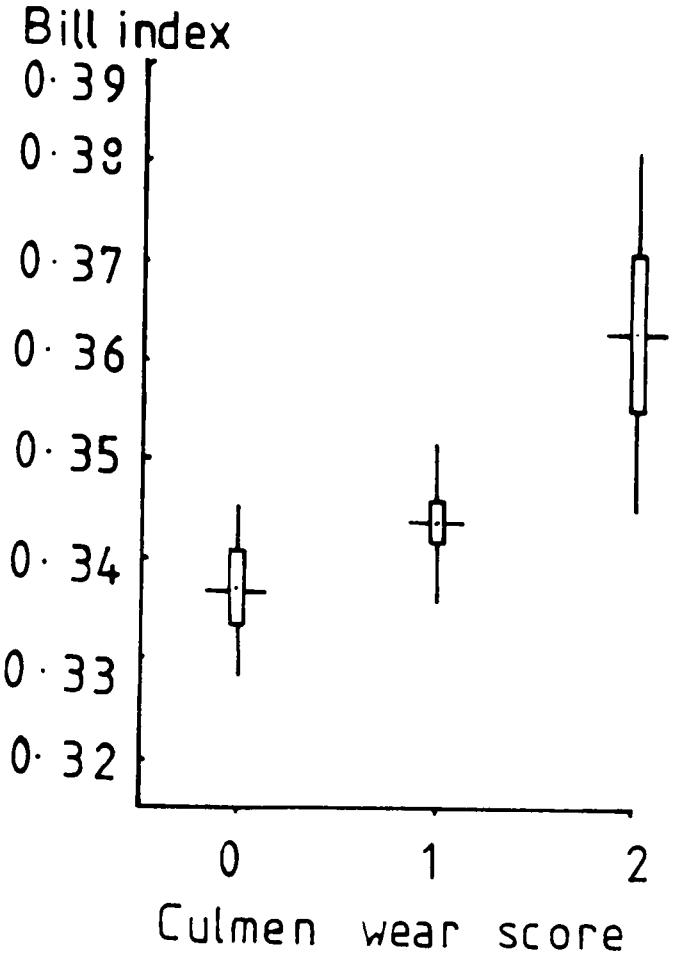


Figure 3.19. Differences in the level of culmen wear scored from photographs in relation to bill index in 30 Great tits. The figures show means ± 1 s.e. (block) and ± 95% confidence interval (bar). Significantly more wear was observed on relatively deep bills than on relatively narrow ones.

Table 3.25 Correlations among bill characters within sexes for 30 individuals photographed in the winter of 1983/84.

Males (n=17)

	Bill Length	Bill Depth	Bill Index	Index of curvature
Bill Depth	-0.263			
Bill Index	-0.744	0.840		
Curvature	-0.359	0.468	0.525*	
Wear Score	-0.471	0.576*	0.666**	0.446

Females (n=13)

	Bill Length	Bill Depth	Bill Index	Index of Curvature
Bill Depth	0.526			
Bill Index	-0.349	0.613		
Curvature	0.330	0.678**	0.441	
Wear Score	0.321	0.275	0.000	-0.194

Combined (n=30)

	Bill Length	Bill Depth	Bill Index	Index of Curvature
Bill Depth	0.223			
Bill index	-0.395	0.807		
Curvature	-0.112	0.419*		
Wear Score	-0.162	0.437*	0.514**	0.252

than those of males. This sex difference in wear complements the earlier observation that males increased in bill depth between summer and winter while females did not. This suggests that the greater wear shown by males resulted in a compensatory increase in bill depth. The reason for this sex difference is discussed further in chapter 4.

Between winter and summer, males showed a reduction in bill depth, and both sexes showed an increase in bill length. The change in bill length may be attributed to the relaxation of wear at the bill tip as the birds fed increasingly on relatively soft invertebrate food. However, the reduction in bill depth is not explicable in these terms.

On the 29th of March 1984 it was noticed that two adult males (out of six Great tits trapped) showed surface shedding of the bill. The culmen appeared stepped where the surface was flaking off. Further observations showed that this bill moult started at either the bill tip and proceeded proximally or commenced at or near the naso-frontal hinge and proceeded distally (see Plate 3). From that date onwards the presence of bill moult was recorded. During the summer of 1984, moult was observed in 26.5% (45/170) of individuals handled. During the following winter only one individual showed bill moult (0.5%). Figure 3.20 shows that the incidence of bill moult in summer was significantly correlated with bill index and was therefore observed particularly in males. Of 45 birds undergoing bill moult during the 1984 summer, 34 (75.6%) were males. This difference between sexes was highly significant (Binomial test, $P<0.001$). In the 1985 summer, only 29 out of 128 (22.7%) individuals showed bill moult. Of these, 22 (75.9%) were males.

Howard (1951) reported the behaviour of a male Great tit which substantially reduced the length of a badly overgrown upper mandible by bill wiping. This occurred prior to breeding, and Howard suggested that this may

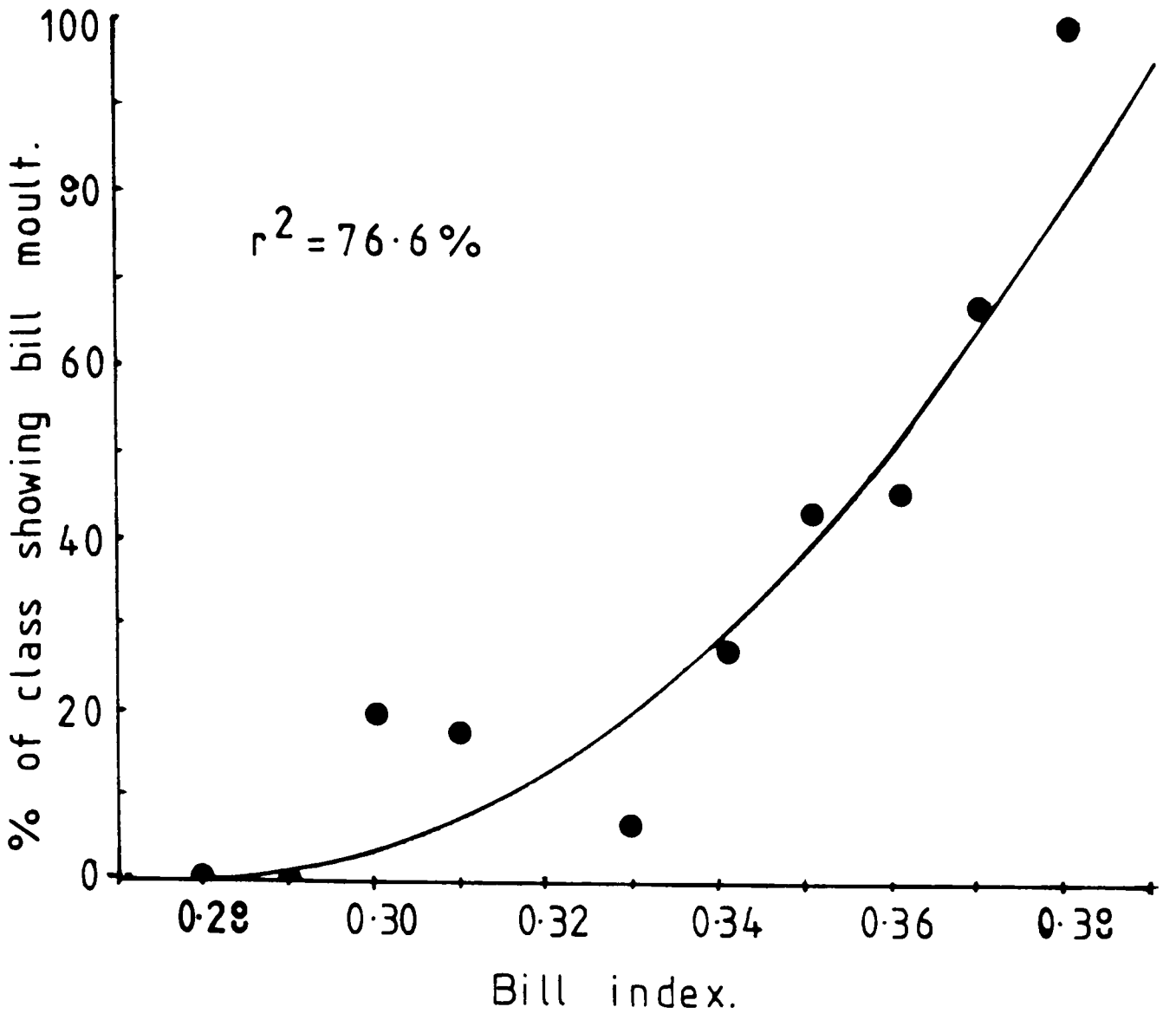


Figure 3.20. The relationship between bill index and the percentage of birds undergoing bill moult during the summer of 1984. A squared relationship was fitted using the least-squares regression method. Within the limits set by these data, the curve $Y=(-25.5+90.6X)^2$ gives a significant description of the relationship explaining 76.6% of the variation.

have been necessary to feed the young since by the following winter the bill was again overgrown. Hinde (1952) noted that bill wiping in the Great tit was particularly common in spring when it was often observed as a displacement activity during agonistic interactions (and therefore particularly in males). Clarke (1970) surveyed the occurrence of bill wiping in different orders of birds. Bill wiping was noted in 77 passerine species. Amongst the functions of bill wiping, Clarke suggested that it plays an important part in honing the bill in species with indeterminate growth of the rhamphotheca. In this respect, it is interesting that he notes the absence of bill wiping in Anseres and soft-billed waders which show determinate bill growth (Rawles 1960). Clarke further suggests that bill wiping must be selectively advantageous as much time and energy may be expended in this activity.

To test for an association between bill wiping and bill moult in breeding adult Great tits, each bird was watched closely for ten seconds after it had found a perch on release. The presence or absence of bill wiping was recorded during this period. Since not all birds were visible after release, the sample size available for this was less than the number of birds handled. Table 3.26 shows the association between bill moult and bill wiping in breeding adult Great tits during the summers of 1984 and 1985. In both years the association was highly significant. Three hypotheses might be suggested to explain this relationship:

(1) Bill wiping is under the control of the individual and bill moult results from wiping so that bill size is actively adjusted by the individual.

(2) Bill moult occurs automatically when the bill reaches a particular size (eg: index), for example due to the greater curvature

Table 3.26 The association between bill wiping and bill moult in breeding Great tits over two years. See text for more details.

1984

	Wiping	No Wiping	
Bill Moult	25	9	34
No Moult	9	89	98
	34	98	132

X^2=54.65
P<Ø.ØØ1

1985

	Wiping	No Wiping	
Bill Moult	13	3	16
No Moult	12	58	7Ø
	25	61	86

X^2=25.96
P<Ø.ØØ1

implied by high bill index. Bill wiping then serves simply to clean off the flaking nail.

(3) Bill moult occurs automatically under hormonal control in spring. Its association with bill wiping is then as under (2) above.

Since high (indeed higher) bill indices occur frequently in winter when bill moult is absent, hypothesis (2) may be rejected. If bill moult was under hormonal control it might be expected to show a more specific phenology. In 1984 the incidence of moult in males declined significantly with date (r_{10}=-0.816 (n=12 x 2 day periods),P<0.01). This is shown in Figure 3.21. In 1985, no significant correlation occurred between moult and date. Although a combination of hormonal control and bill index has not been rejected this is unlikely to be the cause because since daylength is the principal factor controlling the onset of reproductive condition (by its effect on hormone levels) in passerine birds (Follett & Goldsmith in Campbell & Lack 1985), one should not expect the incidence of moult to vary so greatly between years. Hence it is most probable that bill wiping itself causes bill moult. In this respect, bill moult is simply an increased level of wear, but the distribution of the wear surfaces is quite different from that observed at the tomia, and caused by feeding. Differences between individuals in the occurrence of wiping suggest that it may be under conscious control. Hence active regulation (within the constraints of growth rate) of bill size by the individual is probable.

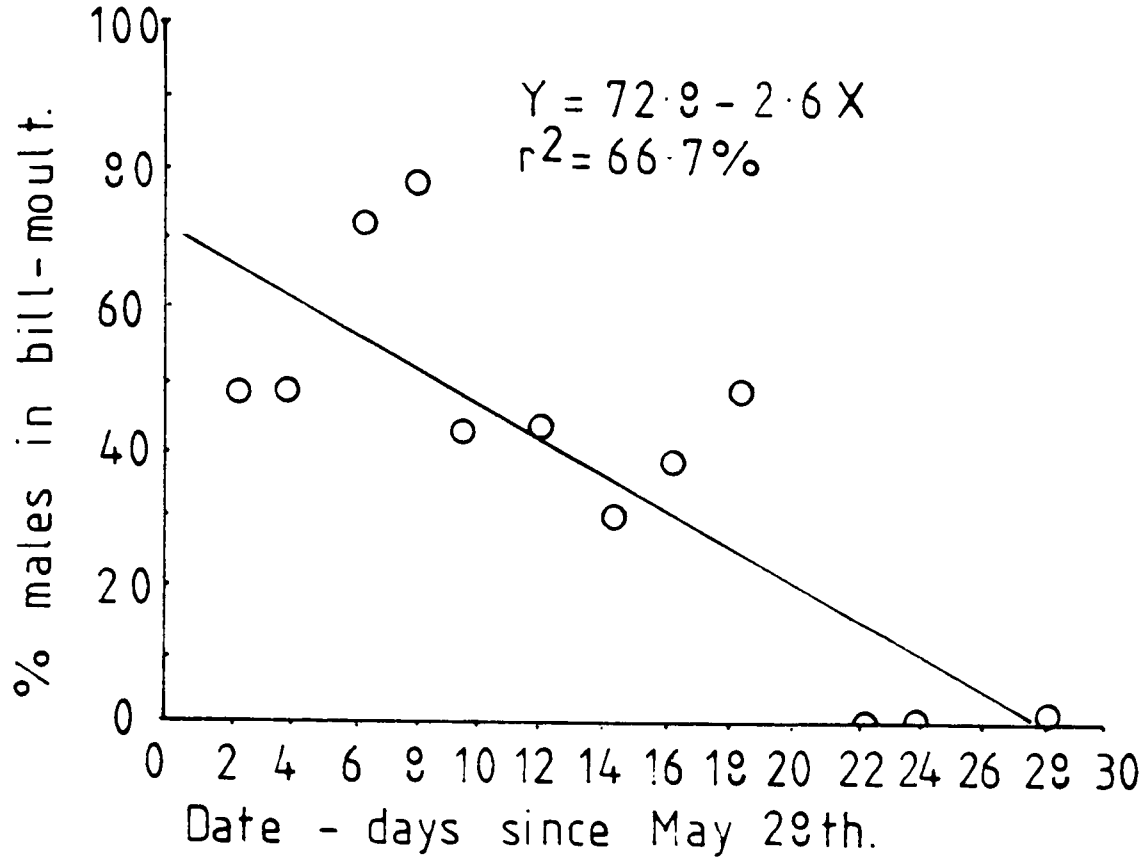


Figure 3.21. The decline in the percentage of male Great tits in bill moult with date through the summer of 1984. Data were grouped by two-day periods.

3.8 Summary and discussion.

Whilst the size of the skeletal components of the rostrum are strongly correlated with body size in the Great tit, and therefore presumably show a heritability of about 75% as does body size (Garnett 1981), the rhamphotheca shows indeterminate growth. Hence although the size of the underlying bone constrains the minimum size of the bill, the maximum length is not so determined. Indeed the fact that male bill length averages less than that of the female whilst body size is greater, suggests that bill length may vary more or less independently of the length of the supporting bone. In other words, most of the variance in bill length is determined by variance in the rhamphotheca. This does not mean that bone size is irrelavent to bill length as the maximum length may be constrained by the strength of the bone, and this is itself a function of bone size (Bock 1966). Since bill characters show about 50% heritability, it is unlikely that they are entirely independent of bone and body size. However, the principal theme of this chapter has been the strong influence that the immediate environment has on bill size ("immediate" because of the relatively small contribution apparently made to the final bill size by the growth environment of the nest).

Table 3.27 gives estimates of the percentage of the bill variation explained by each of a series of factors included in this chapter. These were calculated by single classification ANOVA within each season type (summers, springs etc). Hence the estimates include the effect of covariance among factors (e.g. interaction of age and sex) although this is small relative to the total variance explained. Hence r^2 values should not be summed to give a total explained variance. However, the estimates are largely independent of the heritable component of variation and give a reasonable guide to the

Table 3.27 The relative importance of age, sex, origin and season to bill variation in the Great tit. Values given are the percentage of total variance explained by that factor in a single classification ANOVA.

(i) Variance explained within seasons.

Summer	Age (residents only)	Sex	Imm / Res.
Bill length	Ø.49	6.9Ø	Ø.71
Bill depth	Ø.76	2Ø.Ø4	1.99
Bill index	Ø.32	26.34	2.48

Autumn	Age (residents only)	Sex	Imm / Res.
Bill length	1.64	5.54	Ø.33
Bill depth	6.Ø4	39.22	2.32
Bill index	6.Ø2	19.ØØ	1.81

Spring	Age (residents only)	Sex	Imm / Res.
Bill length	7.75	Ø.12	1.27
Bill depth	3.63	24.Ø4	3.28
Bill index	8.21	15.44	3.17

(ii) Variance explained by season - (a) among all seasons. (b) among season types.

(a)	(a) All seasons (ie 1Ø classes)
Bill length	19.1Ø
Bill depth	15.Ø7
Bill index	24.36

(b)	(b) Among season types (ie 3 classes)
Bill length	11.46
Bill depth	1.81
Bill index	6.58

relative importance of each factor. It is therefore, probably an adequate summary.

Within season types, the greatest cause of variance was sex, which may explain as much as 40% of phenotypic variance in bill depth. Its weakest contribution was made to bill length, but its influence here was considerably stronger in summer than in winter. The variation in the contribution made by sex to a given character indicates that part of the environmental component of bill variation was sex-specific. Age was the next most important factor although never contributing more than 10% to the variation in bill size. Its influence was independent of ontogenetic growth which was complete by the autumn. Age contributed up to 25 times more to bill variation in spring than it did in summer. There was a sex component here since only male bill size was significantly influenced by age. The origin of the birds (immigrant / resident) was of little importance in determining bill size.

Up to a quarter of the total variation in bill index could be attributed to differences between seasons. This was greater than the seasonal effect on either of the component characters as they were themselves poorly correlated. The variation due to season was up to eight times greater (in bill depth) among season types than within them. This suggests some constancy in the effect of season type. The variation that was due to differences between seasons was at least as great as the variation due to sex within seasons, although males tended to vary more in bill depth (and therefore in bill index) between seasons than did females. This again indicates the differential effect of environment on the sexes.

The increased age-specific variation in winter contributed to a greater environmental component of phenotypic variation in winter than in summer, suggested by depressed heritability estimates over two winters. In winter

also, the strength of the correlation between bill depth and body weight depended on whether or not the birds were feeding principally on beech mast.

Most of the observations described in this chapter may be explained by non-adaptive (ie: having no bearing upon individual fitness through feeding efficiency etc.) changes in the rhamphotheca resulting from variation in the rates of growth and wear between sexes, ages, seasons etc although observations on the role of bill wiping suggest a means of active bill determination which could be adaptive. Since keratin hardness should not vary between individuals (Frenkel & Gillespie 1979), this suggests that there may be niche differences among groups (age, sex etc). Indeed, only the compensatory dependence of growth rate on wear rate may be a truly adaptive phenomenon and this is clearly a widespread physiological response not restricted to the Great tit! The next two chapters consider whether bill size variation due to age, sex or season is adaptive, that is, whether individual fitness is related functionally to bill size.

Chapter 4. Bill size and ecology - evidence for adaptation in winter.

"A survey of earlier studies of avian anatomy and adaptation reveals that the adaptive significance of very few features of birds has actually been shown."

W.J. Bock, 1977.

Chapter 4. Bill size and ecology - evidence for adaptation in winter.

4.1 Introduction.

Bock (1977) has pointed out that few 'adaptive' traits, (ie: the advantage to the individual of a given character state (either to immediate fitness (survival) or inclusive fitness (survival of offspring etc)) have been demonstrated. This applies particularly to studies of bill morphology where the self evident adaptive value of gross morphological differences among higher taxa has led to the acceptance that all bill characters are adaptive (eg: Bowman 1961). The view (that all traits are adaptive) is a relatively recent and rather dramatic change of emphasis (see introduction). In a criticism of the "adaptationist programme", Gould and Lewontin (1979) pointed to some of the shortcomings of this approach. In particular, they noted that 'design constraints' originating either from mechanical limitations of the phenotype, allometry or genetic constraints of the 'bauplan' etc may lead to non-adaptive character states which could be highly conservative in expression. Further, correlations among characters due to genetic linkage, pleiotropy, etc, could lead to the selection of non-adaptive character states by the selection for adaptive characters with which they were linked. Grant (1985) has shown that directional selection for one bill character in Geospiza conirostris may be buffered by selection in an opposing direction for another correlated bill character. Gould & Lewontin further pointed out that not only need selection not act adaptively, but also adaptation need not be the product of selection since "Good design may be environmental in origin ie: affecting the phenotype not the genotype..", but in this case

selection may favour such phenotypic plasticity itself (Bradshaw 1965).

Studies of adaptation may be divided into two types. The first are those concerning adaptation that involves genetic changes. Bock and Wahlert (1965) termed this 'evolutionary adaptation'. The second are those that represent a direct phenotypic response that may be non-genetic. Bock and Wahlert termed this 'physiological adaptation' although the concept should be extended to include adaptive traits such as learnt behaviour. It is not necessarily possible to separate these under field conditions since selection may cause phenotypic plasticity (the capacity for physiological adaptation) to itself be evolutionarily adaptive. This and the next chapter examine the variation described in chapter 3 in terms of evolutionary and physiological adaptation. Since both environmental covariance with - and high heritability of - bill characters have been shown in this study, both adaptive modes are possible. Evolutionary adaptation is also considered further in chapter 7 on natural selection.

Strong evidence for the adaptive nature of bill variation in the passeriformes comes from the recurrence of character states among widely disparate taxa which share a common ecology (that is, convergent or parallel character states). Most obvious amongst these is the relatively short, deep bill of seed-eaters compared with the relatively long, thin bill of insectivores. Omnivorous species tend to be intermediate in this respect (see Lack (1971) for a general survey). Congeners (eg: Parus) which differ with respect to their niche along this insect/seed gradient may show bill index variation which parallels that which is observed among higher taxa. Similarly, species showing a seasonal shift along this gradient may show a parallel shift in bill index (Davis 1954) as I have shown in the Great tit.

There are many convergent characters of the bill and associated skeleto-

muscular components of the kinetic skull which are associated with the insectivore/granivore dichotomy. A number of these are summarised in Table 4.1. Many of these are not independent character states, but are correlated components of a highly coordinated character complex. For example, the curvature or convexness of the culmen is a function of the bill index which is itself a function of bill depth. The muscle mass is limited partly by the size of the attachment points such as the orbital process of the quadrate and palatine process of the premaxilla. However, there is room for compromise amongst 'characters' and it is informative to examine the Great tit skull in view of the general pattern.

Figure 3.1 shows the Great tit skull. In general morphology, the bill is intermediate between the typical seed and insect feeders although seasonal variation shifts its relative position with changes in diet. In general features of its design the bill is intermediate. However, seeds are held in the feet and hammered with the bill rather than being compressed between the mandibles as occurs in finches and buntings. Hence although bill strength and depth are undoubtedly related to each other in the Great tit, the direction of stress on the bill should differ markedly from that of a typical seed eater such as a finch. Scarring on the culmen described in chapter 3 results from mast foraging both when seeds are extracted from the woody husk (the bracts which surround the seed when ripe), and when opening the hard testa. Considerable force may sometimes be necessary to remove a seed from its husk (though most seeds are dropped from the husk while the latter is still on the tree). While not as painful as the Blue tit, the pecking power of the Great tit is almost legendary!

Anatomically the mandibular apparatus combines features commonly seen in both insectivorous and granivorous birds. The muscle mass is intermediate in

Table 4.1 Bill character differences among insectivorous and granivorous passerines summarising the general principals of bill design.

Character	Granivore	Insectivore	Reference
(1) General morphology.	Short & deep = strong & slow.	Long & thin = weak & fast.	1,7.
(2) Design principle.	Power.	Speed.	2
(3) Culmen Gonys.	More convex [1]	Less convex [1]	5
(4) Specialisation between taxa	Less [2]	More [2]	5
(5) Bill Length	Covaries positively with seed size & hardness	longer bill better for handling mobile prey & allows more rapid closure.	1,2,9,11, 12,13,14.
		Covaries positively with prey size.	7,16
		Covaries negatively with prey size.	8,10
		Covaries with variance in prey size.	6,8,10
(6) Bill Depth	Increased = strong bill	reduced = weak	2,12
(7) Muscle mass relative to skull	Large	Small	1,
(8) Adductor muscle fibre histology.	Pinnate [3]	Parallel [3]	1,2,15.
(9) Orbital Process of Quadrate.	Long [4]	Short [4]	2.
(10) Palatine process of premaxilla.	Large [5]	Small [5]	3.
(11) Angle between commisure & jugal.	acute	obtuse [6]	2,4.

N.B: See next page for notes.

Notes to Table 4.1

1. Convexness is related to the bill index. Within insectivores it is highest in bills that grip, lowest in those that probe (Bowman 1961).
2. In granivores most variation is in size and correlates with seed size. There are notable exceptions such as Loxia. In insectivores variation for probing, flycatching, gleaning etc and there is size variation relating to prey size within these guilds.
3. Pinnate fibres give slow powerful contraction. Parallel fibres give rapid but weaker contraction and a wider gape.
4. Gives area of muscle attachement if large, gives low kinesis, and low bill tip speed, if small, gives high kinesis and high bill tip speed.
5. Muscle attachement for M. pterygoideus which depresses the upper mandible. In granivores, although kinesis is reduced, the process prevents deformation of the upper mandible while feeding, so preventing damage to the naso-frontal hinge. In insectivores, although kinesis is high, the force exerted on the bill are weak, hence the process is reduced (eg:Parus) or absent (eg:Certhia, Sitta).
6. In woodpeckers the angle is straight (180^{o}).

References.
1) Beecher 1951, 2) Beecher 1962, 3) Bock 196Ø, 4) Bock 1966, 5) Bowman 1961, 6) Grant 1968, 7) Greenberg 1981, 8) Herrera 1978, 9) Hespenheide 1966, 1Ø) Hespenheide 1973, 11) Kear 1962, 12) Lederer 1975, 13) Morris 1955, 14) Newton 1972, 15) Potapova & Panov 1977, 16) Williams & Batzli 1979.

In addition to these characters, the intestine tends to be longer and the gizzard more muscular in seed eaters than in insectivores (Bowman 1961).

size (relative to the size of the skull) between those observed in the strict insect and seed feeders, and the adductor muscles appear to be mildy pinnate. The orbital process of the quadrate is reduced as is the palatine process, both being features generally associated with an insect diet. The angle made by the junction of the commisure with the jugal bar is very obtuse to almost straight. In this it is more like a woodpecker than an insectivore.

In the last chapter I showed that most of the variation in bill index among individuals within seasons was contributed by sex. In winter this occurred partly by a shortening of the bill in males (especially adult males), but also by a significant difference in bill depth which was sometimes absent in summer. In summer, bill length contributed more to the sexual dimorphism in bill index so that a seasonal difference in the relative importance of bill length and depth occurred. This pattern also accords with the seasonal variation in diet, emphasising bill length in summer and bill depth in winter. The observed sex difference in winter suggests that females might take a more insectivorous diet than males at that time. Section 4.2 examines sex differences in the winter niche.

4.2 Intraspecific variation in the winter niche.

This section examines the variation in winter niche of the Great tit at Wytham and in particular, attention is given to sex differences in foraging niche. An attempt will then be made to relate this variation to that observed in bill size and shape in winter, and particularly to sexual dimorphism.

The foraging niche of an animal may be defined in terms of a number of dimensions corresponding to the type and location of food (Hutchinson 1957). Hence feeding height, feeding method, the proportion of insect food in the diet, and prey size have all been used to define niche space in Parus (introduction). Correlation amongst niche dimensions may allow most niche variation to be adequately described by a single dimension. MacArthur & MacArthur (1961), MacArthur et al. (1962,1966), Recher (1969), Karr & Roth (1971), Terbough (1978) and Moss (1978) all found that foliage height diversity explained a major part of the variance in bird species diversity in forests as dissimilar as tropical America, Australia and Scotland. A major component of foliage height diversity is the vertical zonation of vegetation. Colquhoun & Morley (1943) showed that this zonation in temperate Oak woodland allowed niche segregation among Parus species. In Parus in winter at Wytham, feeding height covaries with a niche gradient from mast foraging on the ground to invertebrate foraging in the trees (Hartley 1953, Betts 1955). For these reasons, I have concentrated on foraging height as the major indicator of niche variation in the present study. A brief review of winter niche occupancy in Parus was given in chapter 1.

4.2.1 Methods.

To examine winter niche variation, observations were made of all tit flocks encountered during regular walks around the study site (Figure 2.1) between 10.00 and 16.00 hours. The approximate size and species composition of parties were recorded together with the sex, feeding height, feeding method and substrate of Great tits in the flock. The data were obtained during approximately 250 hours of observation over the three winters.

Great tits are readily sexed in the field on the width of the belly stripe. Birds feeding on or near the ground were easily observed at close range. Birds feeding higher in the trees were observed from below only so that sexing was facilitated. Less than 10% of birds observed were unsexed. Although no bias is expected in the ability to sex birds at different heights, there may be bias in the ability to find birds at different heights. Hence the height categories used may not be directly comparable for estimating the relative use made of each height class. The feeding height categories used were based on those of Colquhoun & Morley (1943) and Elton (1966). Feeding height was recorded as follows:

1 0-30cm above the ground (herb zone).

2 Lower shrub bole zone.

3 Upper shrub bole or shrub canopy zone.

4 Standard tree dead branch zone.

5 Standard tree canopy.

(see also Figure 4.1). During the winter of 1982/83 feeding method was described as gleaning, probing or hammering (and upon what). Tree species and

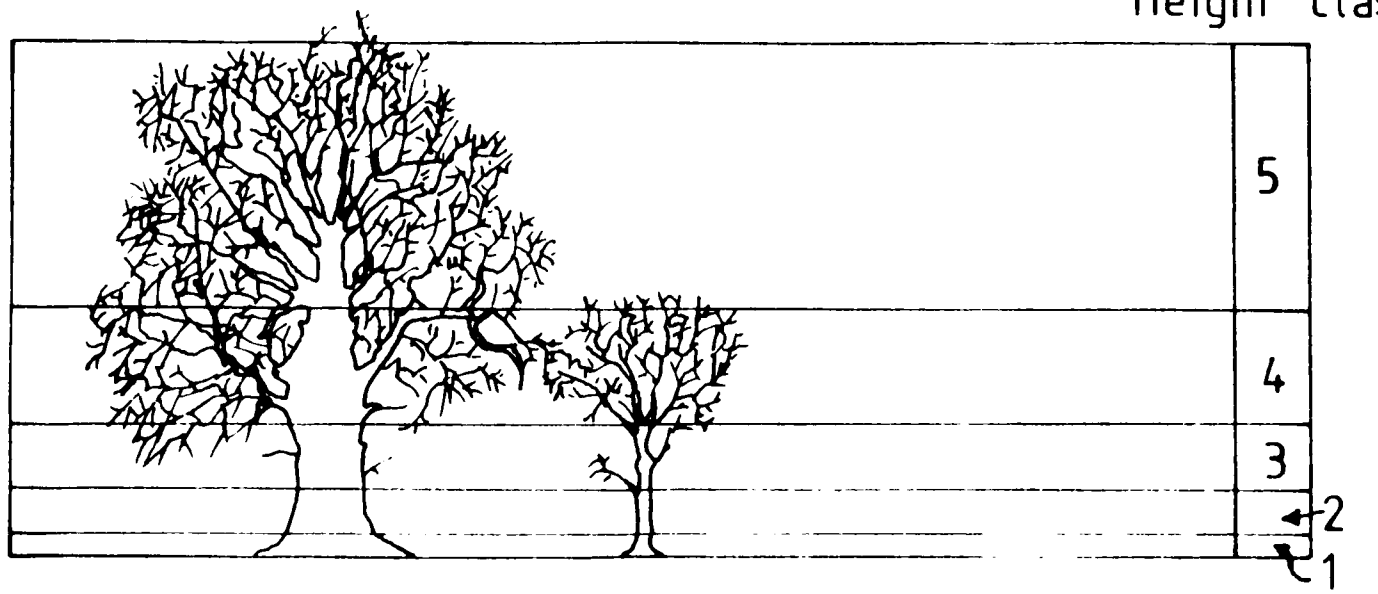


Fig. 4.1 Height categories used in tit flock observations.

location (bole, branch or twigs) were also noted. Flock observations were recorded on a dictaphone.

To examine dietary differences between sexes, faeces obtained while mist netting in the winter of 1984/85 were collected and analysed under a dissecting microscope. The main aim of this was to determine whether differences existed in the proportion of invertebrates taken. The abundance of invertebrate remains in the sample were estimated on a 6 point scale for each of the following classes: Arachnida, Diptera, Coleoptera, Hymenoptera and others. The scale used was:

0 none present.

1 1-10 items.

2 11-25 items.

3 26-50 items.

4 51-100 items.

5 >100 items.

The scores were then summed for each sample to a possible maximum score of 30. Samples were analysed 'blind' with respect to the origin. There was no significant difference in the date or time of collection for male and female samples and all samples came from the same site. No attempt was made to estimate the plant content of the samples although much plant tissue was present in all. Gibb (1957) presented some evidence that plant and animal remains passed at different rates through the Great tit gut. Hence feacal sampling is a poor way to assess the plant component of diet (Mook & Marshall 1965). Nine male samples and nine female samples were collected.

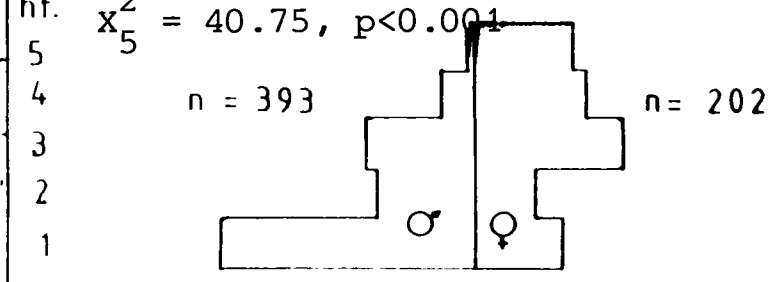
4.2.2 Results and discussion.

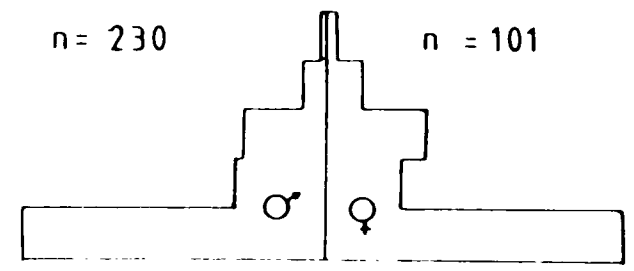
The distribution of foraging tit flocks varied markedly between winters depending on the distribution and abundance of beech mast and the availability of invertebrate food. Two main beech feeding areas, differing markedly in physiognomy were identified. The first, Rough Common (r in figure 2.1) consisted of Oak, Beech, Sycamore, Ash and Lime with a well developed understorey of Hazel, Blackthorn and Elder underlain by Bramble. The second, Brogden's Belt (b in figure 2.1) was a pure Beech stand with a sparse understorey of Elder. Since Beech maintains a relatively poor invertebrate fauna in Britain (Kennedy & Southwood 1984), opportunities for foraging in the leafless canopy were severely limited in Brogden's Belt. Most observations from above level three in Rough Common came from tree species other than Beech. Table 4.2 summarises the principal differences between sites and the distribution of Great tits at those sites in the three winters. In two of the three winters, females fed significantly higher than males.

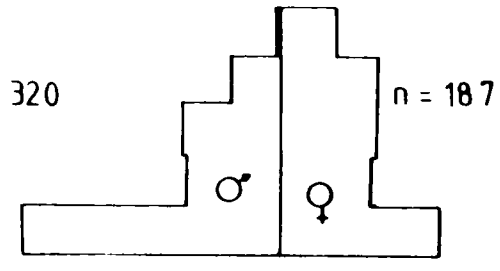
Figure 4.2 shows the distribution of feeding stations and feeding methods used during the winter of 1982/83. Feeding height and method were strongly correlated. Most seed hammering occurred nearer the ground (mean height = 1.75 ± 0.97) whilst probing and gleaning were observed mostly at higher levels (mean height = 4.86 ± 0.90 and 4.30 ± 0.82 respectively). This difference was highly significant (Kruskal-Wallis test corrected for ties, $H=27.329$, $P<0.001$). The results of the faecal analysis are presented in table 4.3. Averaged over all classes, female samples contained significantly more invertebrate food than males. This agrees with the difference in feeding height and method.

Table 4.2 Food availability and Great Tit distribution in the three winters.

WINTER	SEASON	SEED ABUNDANCE* R.Common	SEED ABUNDANCE* B.Belt	GREAT TIT DISTRIBUTION.	FEEDING OBSERVATION
1982/83	Autumn	>200	<10	>80% of Great Tit observations from Rough Common. Due to a late leaf-fall, feeding high until December when they moved onto beech mast.	$x^2_5 = 40.75$, $p<0.001$
	Spring	>200	<10		n = 393 n = 202
1983/84	Autumn	<50	>200	>80% of Great Tit observations from Brogden's Belt till December. Then high emmigration rate. Rough Common territory holders stayed on territory throughout the period.	$x^2_5 = 1.62$, n.s.
	Spring	<10	<10		n = 230 n = 101
1984/85	Autumn	>200	<50	Due to excellent and late soft fruit crop, tits moved onto beech mast late in November. >80% of observations in Rough Common. Flocks of up to 200 birds caused severe depletion by January.	$x^2_5 = 15.45$, $p<0.01$
	Spring	<50	<10		n = 320 n = 187







* Seed abundance is given as a minimum estimate of seeds m^{-2} at the start of the season.

Fig. 4.2 Great tit flock observations - winter 1982 / 83.

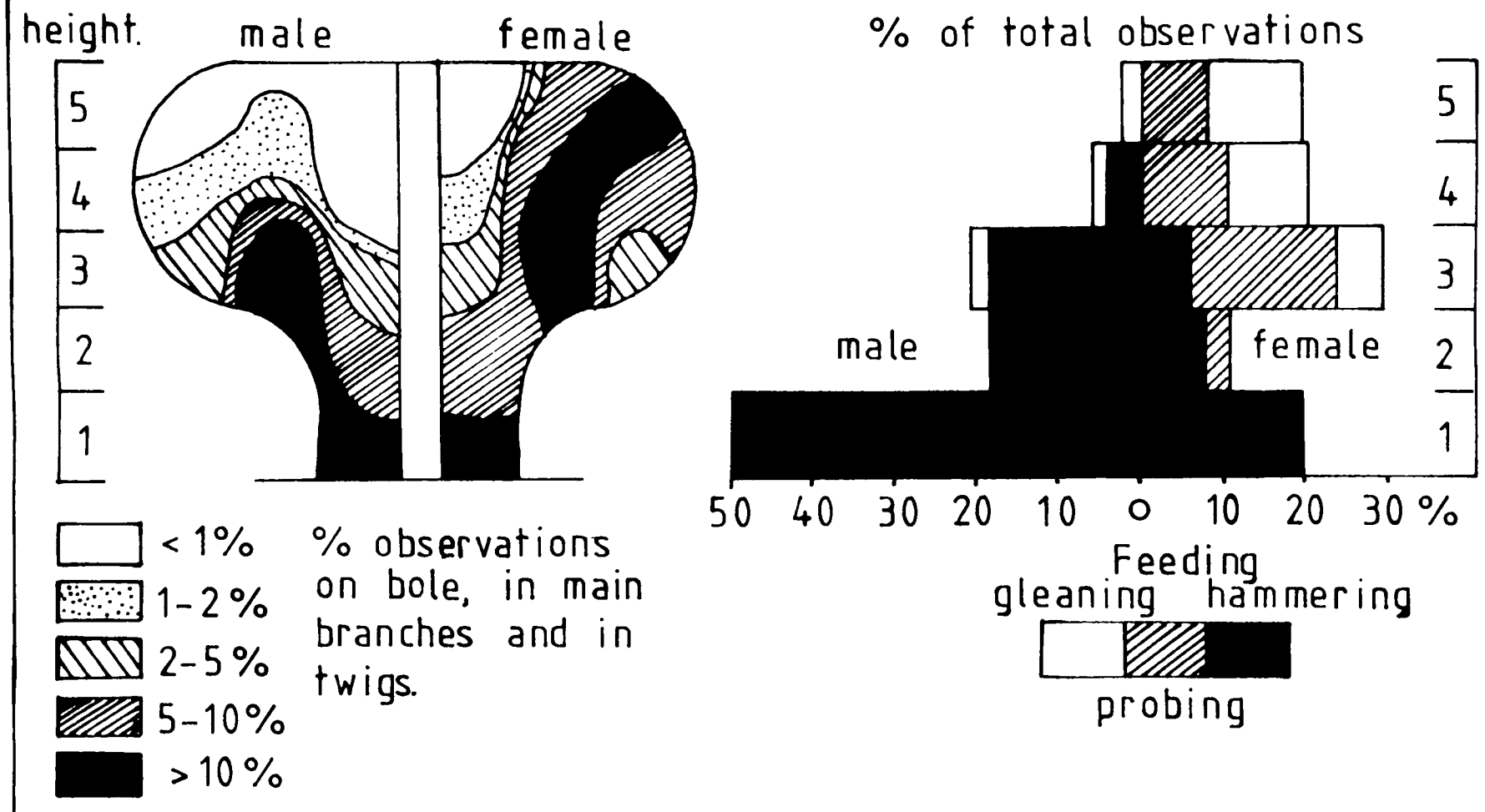


Table 4.3. Mean invertebrate scores (± 1 sd) in faecal samples from 9 male and 9 female Great tits obtained during the winter of 1984/85. T test values are given for comparisons between sexes in each class. Note that the sex difference for the total score (ie: over all classes) was significant at the same level when compared by Mann-Whitney U test.

Sex	Arachnid	Diptera	Coleopt.	Hymenop.	Other.	Total Score.
Male	1.89±Ø.93	Ø.67±Ø.87	Ø.56±Ø.73	Ø.62±Ø.87	Ø.11±Ø.33	3.89±2.57
Female	3.67±1.5Ø	1.11±1.17	1.78±1.64	Ø.33±Ø.71	Ø.44±1.Ø1	7.33±3.61
t_{16}	3.Ø2	Ø.92	2.Ø4	-Ø.89	Ø.94	2.33
P<	Ø.Ø1	Ø.37	Ø.Ø7	Ø.39	Ø.37	Ø.Ø4

The dominance hierarchy in winter flocks was clearly defined. Of 23 agonistic interactions observed over three winters, 19 involved males supplanting females when feeding low. Several authors have reported that male Great tits are dominant to females and that this is manifested particularly in the form of supplanting attacks during winter foraging (Hinde 1952, Drent 1983). Table 4.2 suggests that when an alternative feeding station was available to females, as occurred at Rough Common in two winters, they readily exploited it and this resulted in a significant difference in feeding height between the sexes. The winter of 1983/84 provided a useful test since during that season, mast feeding was more or less restricted to Brogden's Belt where little food was available from the shrub or standard canopies. No significant difference in feeding height was observed between the sexes in that winter. Further, the spring of 1984 was the only period in which no significant difference was found in bill index (standardised by tarsus length). This lack of dimorphism was due largely to sampling in Brogden's Belt since at Rough Common (where most captures were of adult territory holders) bill index (standardised) was still significantly dimorphic (t_{94}=3.02, P<0.01). Hence sexual dimorphism was site-specific.

The high density of birds in Brogden's belt during the winter of 1983/84 (>200 in October and November) resulted partly from an unusually high breeding density in Wytham in the previous summer (C.M. Perrins, pers. comm.). Rapid depletion of the mast stock resulted so that by February, fewer than 10 seeds m^{-2} remained out of more than 200 seeds m^{-2} that were available in October. A high population density feeding on a rapidly diminishing resource led to unusually high emigration. The mean number of resident Great tits recovered or controlled outside Wytham within one year of hatching between 1958 and 1983 was 1.96±1.74. The total recovery rate for all years

after hatching was 4.24±3.42. During the period November 1983 to March 1984, 32 recoveries and controls were reported. The previous highest being 16 in 1981 following a high breeding density and a severe winter. Of the 32, 18 were controlled and therefore sexed. Sixteen controls were made by a single ringing group in Oxford whose activities had been very constant during the previous ten years. The ranked order of median control dates for these birds was first-year female, adult female, first-year male and a single adult male. The median date of control for females was significantly earlier than that for males (Mann-Whitney U test, W=22.5, $P<0.01$, $n_f=10$, $n_m=8$). This strongly suggests that food was limiting during the winter of 1983/84 and that females, without an alternative niche in which to escape competition from males whilst retaining some access to the beech mast crop, were more stressed than males.

Figure 4.3 shows the relationship between mean feeding height (calculated from flock observations) and mean bill index (of captures made in the same area and during the same period) of males and females during ten 14 day sampling periods across the three winters. The correlation between feeding height (and therefore its strong correlates of feeding method and food type) and bill index in the same period was highly significant ($r_{18}=-0.823$, $P<0.001$). As the period of mast feeding differed in the three winters, the relationship was not confounded by date. The correlation was stronger for males ($r_8=-0.949$, $P<0.001$) than for females ($r_8=-0.785$, $P<0.01$). The graph suggests a close tracking of niche by morphology through time as was suggested by figure 3.14.

Hogstad (1978b) showed that sexual dimorphism in bill length in the Three-toed Woodpecker Picoides tridactylus could be related to a significant sex difference in feeding height. However, the way that morphology and ecology

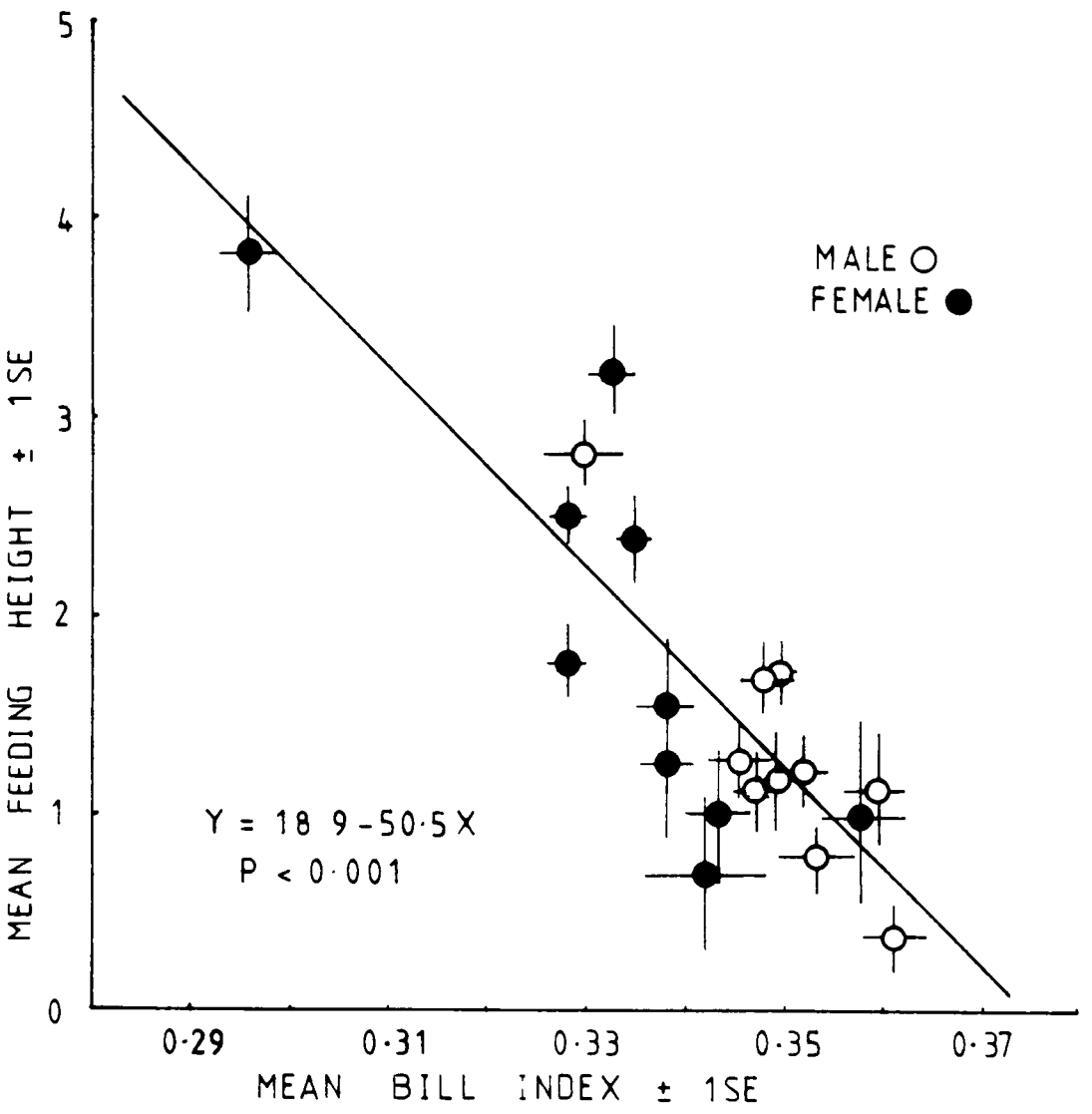


Figure 4.3. The relationship between the mean feeding height of foraging Great tit flocks and the mean bill index of samples of birds measured during the same 14 day period. Data are shown separately for the two sexes and for ten sampling periods across the three winters. Note that the relationship was significant for each sex separately and with the outlyer (top left) removed. There is a strong correlation therefore between foraging height (niche) and bill index.

are related was not clear. He showed also that the degree of sexual dimorphism in four woodpecker species (Picoides tridactylus, Dendrocopos major, D. minor, and D. leucotus) increased with a decrease in niche overlap between sexes (Hogstad 1978$_b$). D. major and D. minor maintained separate winter territories. This allowed a high overlap in resource use and little morphological differentiation. In Picoides tridactylus however, the sexes shared a territory, differed significantly in bill length and showed a great reductin in niche overlap. Williams & Batzli (1979a, 1979b, 1979c) showed similar relationships among members of the bark-foraging guild in Illinois, USA. Hogstad (1978$_b$) used Horn's (1966) definition of niche overlap (Ro):

$$Ro = \frac{\sum(x_i+y_i)\log_e(x_i+y_i) - \sum x_i \log_e x_i - \sum y_i . \log_e y_i}{(X+Y)\log_e(X+Y) - X\log_e X - Y\log_e Y}$$

where X = total number of male observations.

Y = total number of female observations.

x_i = the number of male observations in the ith height class.

y_i = the number of female observations in the ith height class.

This gives a coefficient of niche overlap between 0 and 1 where 0 indicates no overlap and 1 indicates total overlap.

I have applied this formula to the height data presented in figure 4.3. Bill index overlap between sexes may be expressed the mean female bill index as a percentage of the mean male bill index. Figure 4.4 shows a significant relationship between bill index overlap and niche overlap of the sexes across the ten sampling periods. Hence an increase in bill index corresponds to an increase in ground (mast) foraging and the sex difference in bill index was

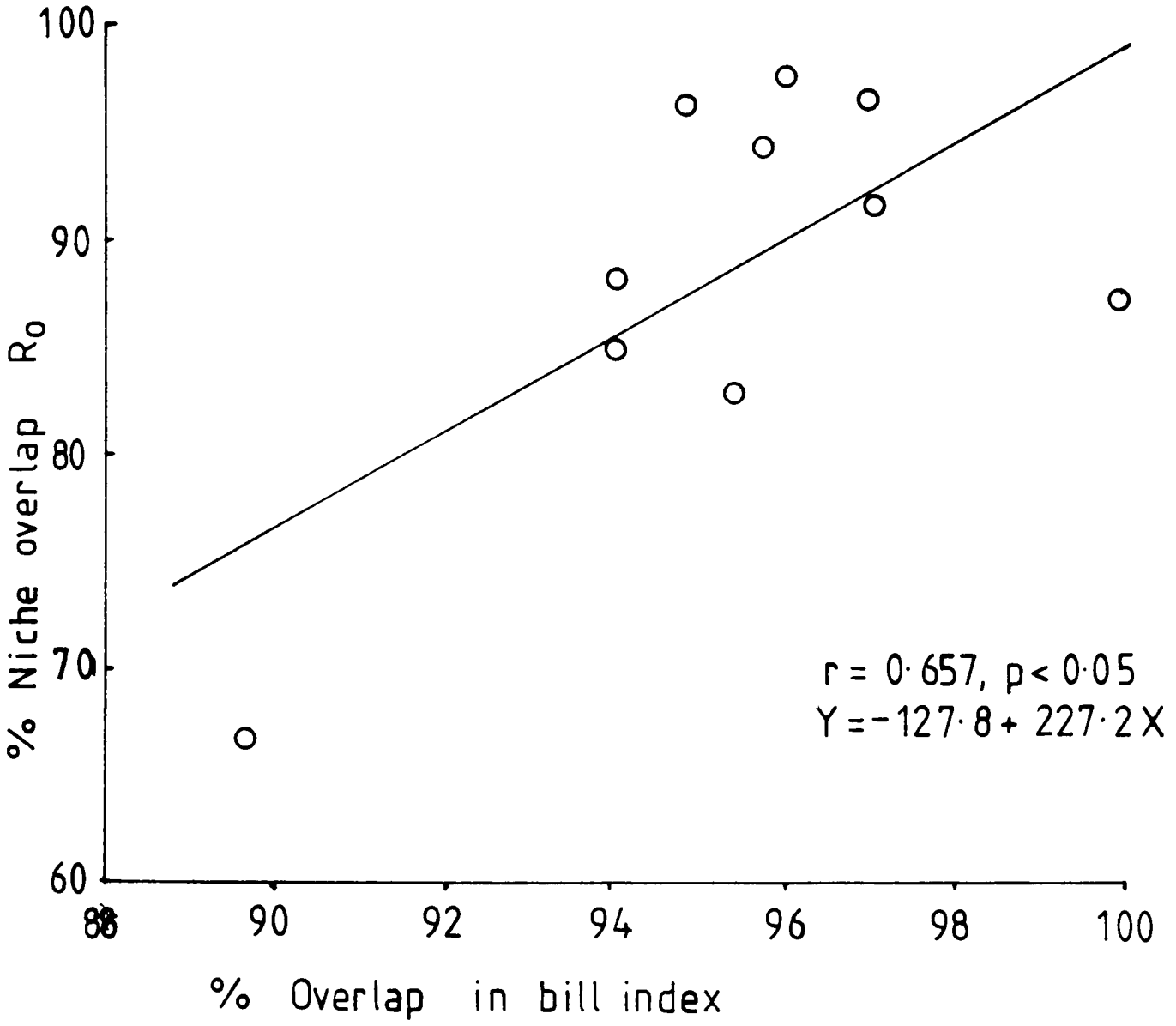


Figure 4.4. The relationship between the relative niche overlap of male and female Great tits (see text for the formula for this calculation) and the relative overlap or similarity of bill index of the two sexes. Data are for the same ten sampling periods used in the analysis of feeding height shown in Figure 4.3.

greatest when feeding height differed most. These results indicate the close relationship between ecology and morphology.

4.3 A laboratory study of bill morphology in relation to feeding efficiency

The results of the previous section suggested that niche differences between individual Great tits were related to differences in bill length and depth. In particular, it was implied that a deep bill (relative to length) was better suited to seed feeding, whilst a narrow bill (relative to length) was better suited to feeding on invertebrate prey. This section examines the relationship between bill size and feeding efficiency (measured as the handling time for a food item) for captive Great tits feeding on different types of food. Since feeding rates depend on a number of factors other than bill size (such as the degree of satiation - see Krebs *et al.* (1983) for a discussion of this) observations were made in the laboratory where such factors might be controlled.

Zach & Falls (1978) studied the food preferences of captive Ovenbirds *Seiurus aurocapillus* and found that they were most selective in their feeding when food was most abundant. To study further the factors affecting prey selection in this species, Paszkowski & Moermond (1984) examined the food handling abilities of five captive Ovenbirds. Energy gain per unit of handling time (E/T_h) was taken as a measure of feeding efficiency (as discussed by Krebs *et al.* 1983). Paszkowski & Moermond considered the influence of prey size, individual differences in behaviour and morphology, satiation and experience on handling time of mealworms *Tenebrio mollitor* larvae. They found that all these factors contributed significantly to the variance in handling time. However, prey size (31.33%) and individual differences among birds (24.39%) explained considerably more of the variance than any other factor. Within birds, on average, prey size explained 43.6% of

variance in handling time. The greatest contributor to individual differences was bill length. Long-billed birds were both significantly faster at handling prey of any particular size class than short-billed birds, and were more efficient (E/T_h) at feeding. Short and long-billed birds differed significantly in their prey size optima, the latter being greater for long-billed birds. They concluded:

"Our experiments suggest that small differences in bill size could significantly influence prey selection, ultimately producing divergent diets under natural conditions".

Paszkowski & Moermond's study suggests strongly that bill length was adaptive in the Ovenbird since age, sex, experience etc were eliminated as sources of variation in handling time. However, it was not clear why a long bill should be better for handling mealworms.

In the Great tit, diet and bill size co-vary seasonally and I have suggested that the two components of bill index may differ seasonally in their relative importance. Hence to relate bill size to handling time for both seed and invertebrate food I have used bill index itself as the principal bill character under investigation. This does not preclude the study of bill length or depth in relation to feeding efficiency.

4.3.1 Methods.

To test whether feeding efficiency was affected by bill index, I brought fourteen Great tits into captivity (under licence from the Nature Conservancy Council) during a cold period in early February 1985. The birds were caught while feeding on beech mast, and those taken were selected from a larger catch on the basis of sex and bill index. The sample contained seven males and seven females showing no sex difference in bill index, but together providing a range of bill indices from 0.310 to 0.365 (see Table 3.1 for the full range of bill indices observed during the study).

The birds were kept in individual $1m^3$ cages in a laboratory at the Wytham Field Station where they were subject to natural daylight and ambient temperature. They were fed daily on beech mast, sunflower seeds, peanuts and a few mealworms. When fed, all the birds ate mealworms before seed indicating their preference for live food when available. Indeed even on the first day, the attraction of mealworms was immediate although they could not have experienced them previously. The birds were tested within five days of capture, and were released where caught within ten days of capture.

On the first day, each bird was given five viable (containing an embyo) and five inviable (empty testa) beech seeds of equal size in a small dish. The next day, I recorded the number of seeds of each type that had been opened. In fact no inviable seeds were opened, and Table 4.4 shows the number of each type removed from the dish. The ten uneaten viable seeds were distributed among seven different individuals, so that the results were not influenced by a small number of birds which could not make a distinction between the seed types.

Table 4.4 The number of viable (containing an embryo) and inviable seeds removed from a dish during the first 24 hours after capture. Data from all birds are pooled.

	Viable seed	Inviable seed		
Removed	60	2	62	
Remaining	10	68	78	X^2 = P<0.001
	70	70	140	

The experiment shows that all of the birds could identify viable and therefore edible beech seed. Further, this recognition was probably made by eye rather than on the basis of seed weight since it is unlikely that inviable seeds would have been replaced in the dish. It should also be noted that when offered seed and mealworms together, every bird ate all of the mealworms before any seed.

Between 10.00 and 16.00 hours each day (starting two days after capture) each bird was deprived of food for one hour. The order of deprivation was randomised among birds. After this, they were each provided with five x 1cm mealworms and five beech seeds of average size. The time taken to eat each mealworm and to open and eat each seed was recorded and taken as a measure of feeding efficiency (c.f. Krebs et al. 1983). Data were collected "blind" with respect to bill measurements and observations were made from within a hide. Although the birds were provided with equal numbers of seeds, observation sample sizes are not equal, due to differences in feeding rates among birds.

When feeding on mast, the birds hammer open a hole in one face of the seed. The contents, (mostly cotyledon in beech seeds) is eaten through this hole and the more or less intact testa is then discarded. When eating mast, peck rates were remarkably constant at about 1 peck per second ($N_{pecks}=0.87+0.96T_h$, $F_{1,31}=333$, $P<0.001$). Since some birds tended to drop seeds more often than others and then take a new seed (a tendency not related to sex or bill size), a correction to total handling time was made by weighing the discarded seed remains. The percentage of a seed eaten was estimated as:

$$\%\ \text{seed eaten} = \frac{\text{Mean seed Wt} - \text{discarded seed Wt}}{\text{Mean seed Wt}} \times 100\%$$

The corrected handling time was then calculated as:

$$T_h' = \frac{\text{Mean handling time per seed}}{\text{Mean \% of each seed eaten}}$$

No such correction was necessary for mealworms as they were all eaten completely.

4.3.2 Results and discussion.

Figure 4.5 shows the mean $\pm$ 1 s.e. of handling time for each bird for (a) beech mast and (b) mealworms, plotted against bill index. In agreement with Sherry & McDade (1982) and Paszkowski & Moermond (1984), I found that exponential rather than linear functions explained more of the variation in handling time. This might be expected as handling time must be asymptotic to bill index. High bill index birds were significantly faster at handling beech mast than were low index birds. The reverse was true for mealworms. In both cases, bill index explained more of the variation in handling time than did either bill length or depth, suggesting that bill index may itself represent a character of functional significance. For a small sample of seeds, the time taken to open the testa was recorded. The correlation between mean opening time and bill index for six birds was -0.803, significant at $P<0.06$. Hence birds with a high bill index tended to be quicker at opening mast. This may be related to the difference in strength between bills. In this sample of fourteen individuals, neither bill index nor handling time correlated either with sex or tarsus length. The birds may be considered of similar experience as (a) they were caught together whilst feeding on mast; (b) all showed experience of mast and could distinguish viable seed; and (c) all preferred live prey when available. Hence the results support the hypothesis that bill index is adaptive and that the seasonal change observed in bill index which parallels the seasonal change in diet, follows the pattern expected if bill index tracks the seasonal change in its optimum value. Further, it suggests that sexual dimorphism observed in winter is related to the observed niche segregation.

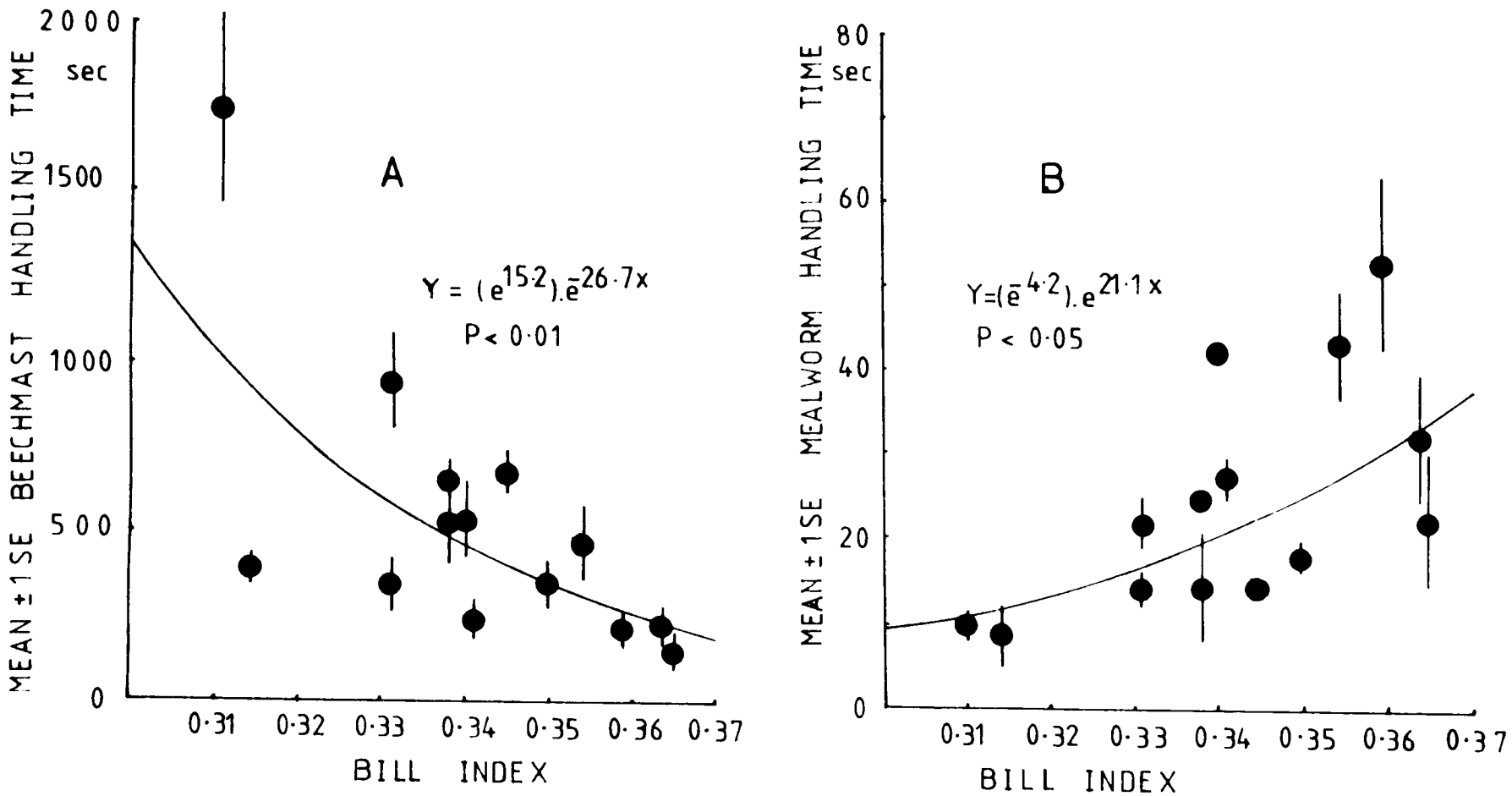


Figure 4.5. The relationship between feeding efficiency (handling time) and bill index in 14 captive Great tits. Figure A shows that relatively deep-billed birds were significantly faster than relatively narrow-billed birds at handling beechmast whilst figure B shows that they were significantly slower at handling mealworms. Note that all birds preferred mealworms when offered a choice. See text for further details.

There may be several reasons why handling times varied with bill index. Willson (1972) showed that in finches, the relative force that could be exerted by the bill correlated more highly with bill depth than bill length. The higher correlation of bill index (than depth) with mast handling time suggests that either bill length also contributed to the variation, or bill index reflects another character such as shape which is itself the most important. Either way, Willson's observation cannot explain these results entirely. Beecher (1962) showed that the insectivore bill could be closed more rapidly than the seed-eating bill, and Lederer (1975) pointed out that a longer bill was better for handling mobile prey. He maintained also that jaw forces in insectivorous birds were only those required to catch and hold prey. Further, if the muscle forces exerted by a finch were applied to an insectivore bill, it would shatter. That is, the insectivore bill was better adapted for capture and handling prey (procurement) while the granivore bill was adapted for food processing. Partridge's (1974) discussion (chapter 1, page 26) may also apply here.

4.4 Bill variation and survival.

The study of bill size adaptation in wild populations is fraught with difficulties due to the confounding effects of co-varying factors. This is especially true of phenotypically plastic characters. To be adaptive, there should exist some advantage in a particular bill size. In a species which is sexually dimorphic in bill characters, this advantage should differ between the sexes. However, selection for a character state is unlikely to be continuous, being more intense under certain conditions (Hespenheide 1973). Hence it may not be possible to detect selection during a short investigation (Endler 1986). This is considered further in chapter 7. However, it may be possible to relate a character of interest to some other factor of known adaptive importance. Its own adaptive importance might then be inferred.

In the laboratory study described above, I have assumed that feeding efficiency gives a measure of adaptive value. Under field conditions, the fat score may give an indication of individual condition, and its covariance with bill variation (if present) could be due to the covariance of both of these variables with feeding efficency. However, the adaptive value of fat storage must first be shown in each age and sex class. Appendix 3 presents observations on diurnal fattening in the Great tit. This suggests that the costs and benefits of carrying fat may differ among age and sex classes. Adults may be buffered in some way against the hardest winter conditions. For example, they can afford to raise their fat reserves less rapidly than young birds with a drop in temperature.

4.4.1 Fat reserves in relation to bill size.

The level of fat carried by a Great tit in winter is a function of the time of day, the temperature, its social status and feeding efficiency (energy gain per unit handling time). In chapter 3 I showed that deep-billed birds of a class were significantly heavier than thin-billed birds when feeding on mast in winter (data presented in Appendix 2). Since seasonal changes in bill size occurred within individuals, two hypotheses might be proposed to explain this.

(1) Birds of a class were heavier because they were larger. Greater size could imply greater social status, hence greater access to mast and subsequently, bill depth might increase as a compensatory response to mast feeding.

(2) Deep-billed birds were more efficient at feeding on mast, deposited fat more rapidly, and were heavier as a consequence.

These hypotheses are not mutually exclusive, but may be tested by removing the effects of body size (tarsus length) in a partial correlation analysis. If the correlation between body weight and bill depth remained significant when body size was kept constant, the latter hypothesis (heavy due to fat) is supported. If the correlation was lost, the former hypothesis (heavy due to size) is favoured. Analysis of weight rather than fat score was used since body weight could be measured more precisely than fat. Partial correlation was carried out on the eight (four male, four female) significant correlations obtained between bill depth and body weight (chapter 3). Six

correlations remained significant though in all cases the significance of the correlation was reduced. The remaining two cases were both male classes. Hence it is likely that both explanations are true to some degree. However, in males, body size, dominance and intraspecific competition may be more important whilst in females, where intra-class dominance is probably less important, fat deposition explained more of the covariance between body weight and bill depth.

To examine further the association between mast feeding and the body weight/bill depth relationship, I divided adult males trapped in Autumn 1983 into two groups:

(a) Territory holders (known to have bred in the vicinity during the previous summer) in the Rough Common area with access to a little beech mast, but partly supported by unpredictable supplemental feeding (see Appendix 3)

(b) Those trapped off their territories whilst feeding on mast at Brogden's belt. No adult male trapped at Brogden's belt during that winter bred there in either the previous or following summer.

This compares similar individuals trapped in the same period under low and high competitive situations respectively. The first group showed no correlation between body weight and bill depth (r_{32}=-0.047) whilst the second group approached significance (r_{19}=0.403, $P<0.07$) with 9.6% of the variance explained. While not a significant difference, there is a suggestion that birds in the two groups responded differently.

4.5 Summary.

The compromise of characters observed in the Great tit bill allows the species to occupy a broad niche. Niche volume varies in time and space and sex differences in niche are mirrored by sexual dimorphism in bill size and shape. Most of the variation so described is "physiologically adaptive" (sensu Bock & Wahrlert 1965) whilst phenotypic plasticity may itself be "evolutionarily adaptive". Bill size influences feeding efficiency in the laboratory and it is implied that this is important in the field also. Hence the sex differences observed in winter represent an optimisation toward different adaptive peaks in the two sexes. Similarly, the seasonal change in bill size results from seasonal variation in that peak as the birds change their diet.

Several authors have suggested that a longer bill allows a greater range of prey size to be taken (Grant 1968, Herrera 1978, - and see final discussion). In the Great tit, the longer bill of the female corresponds also with a more varied niche space and diet. It is interesting in the light of the observations presented in Appendix 3, that a correlation between bill depth and body weight tended to reflect body size in addition to fat store in males. This suggested an interaction between body size and access to food. In females, it always indicated a greater fat reserve. The relationships between bill variation, dominance and foraging strategy will be taken up finally in chapter 8.

Chapter 5. Bill size and ecology - evidence for adaptation in summer.

Chapter 5. Bill size and ecology - evidence for adaptation in summer.

5.1 Introduction

In summer, sex differences explained the greatest part of bill variation in the Great tit. Further, bill length was always dimorphic whilst bill depth was only dimorphic in some years. This, together with previous studies (cited in chapters 1 and 4) suggest that bill length may be more critical than depth to insectivores. Snow (1953) found no significant difference in bill length between sexes in the Great tit. Since they differed significantly in body size, he argued that this indicated the critical importance of bill length in this species. Several workers have noted a relationship between bill length and prey size in insectivorous passerines (Betts 1955, Herrera 1978), although this has rarely been shown within a species (Paszkowski & Moermond 1984). The Great Tit is largely insectivorous in summer (Gibb 1954, Betts 1955). Breeding is timed to coincide more or less with the peak abundance of caterpillars which form the bulk of food fed to the chicks (Royama 1970; Lack 1966; Perrins 1970,1979; Minot 1981). Royama (1970) showed that there was no significant difference in the species of caterpillar brought to the nest by each member of the pair.

Bill length showed the greatest seasonal variation of any bill character. Whilst bill length in summer was not entirely independent of its length in the previous winter, it was more constant between summers than between winter and summer. This suggests that the determinants of bill length in summer were either season-specific or genetically determined.

Since the birds defend exclusive territories in summer, Great tits become

more or less uniformly distributed through the wood. This differs markedly from the 'clumped' distribution of the winter flocks. Hence in summer, intraspecific competition for food may arise more within the territory than between. Minot (1981) has argued strongly that Blue tits compete with neighbouring Great tits for food. If true, it is likely that Great tit parents might also be in competition with each other - competition that might be alleviated by specialising on different prey sizes.

This chapter examines the variation in bill length in summer, concentrating on sex differences within the pair. Evidence is presented for a relationship between bill length and prey size, and evidence in support of Schoener's (1971) model of foraging strategy is given. Finally, the significance of parent bill differences are examined in terms of chick survival.

5.2 Bill size in relation to prey size.

For sexual dimorphism in bill length to reduce intra-pair competition for food, there must be a correlation between bill length and prey size. Table 4.1 summarises the relationships observed between bill length and prey size in insectivorous passerines. A longer bill may allow larger prey to be taken by increasing the gape size - a positive correlation (Greenberg 1981, Williams & Batzli 1979). It may allow smaller prey to be taken by improving the bird's manipulative capacity - a negative correlation (Hespenheide 1973, Herrera 1978); or it may do both, in which case an increase in prey size variance is observed with increasing bill length (Grant 1968, Hespenheide 1973, Herrera 1978).

Prey size may be measured by direct examination of food brought to the nest (Kluijver 1950, Royama 1970, Minot 1980) or by analysis of chick and adult faeces, but it must be remembered that food taken to the nest represents only a part of the food taken by the adults at this time. All three methods have therefore been used in this study, although the most information was derived from analyses of nestling faeces.

5.2.1 Methods.

The study was carried out during the summers of 1984 and 1985. To study the relationship between bill length and the size of prey brought to the young, a prey size distribution was required for each parent. Due to the relatively large sample of birds required for this analysis, direct methods such as nest box cameras (Royama 1970, Minot 1980) or neck collars (Kluijver 1950) were inpracticable. Instead, in both summers, faecal sacs were collected from as many chicks as possible when they were ringed on the 15th day. These were stored in 40% ethanol in the field. Dissection and analysis of faecal sacs provided a caterpillar prey size distribution for each brood (see below). The variation in prey size delivered to a brood could then be compared with the difference in bill length between the parents. A significant positive correlation between these two variables would indicate a ~~positive~~ correlation between bill length and prey size although the functional relationship would remain undetermined. However, the direction of slope of this relationship could be determined from the correlation between mean prey size and mean bill length at nests where the parents were very similar (<0.2mm) in bill length.

In 1984, prey items found in the nest when the parents were trapped were collected. Of 42 items collected, 21 were complete caterpillars. In 1985, parent faeces dropped during handling were collected to attempt a direct comparison of bill length and prey size. However, too few prey remains were found in each dropping for this analysis to be carried out although it did permit a comparison of prey size taken by adults with that fed to the chicks.

The caterpillars collected from the parents were identified in the

laboratory. The overall body length and width of the head capsule were measured to 0.1mm. In addition, the mandibles were dissected out and the length recorded to 0.1mm using a low power binocular microscope. Table 5.1 gives the correlation coefficients among the three caterpillar characters in 21 intact caterpillars. Correlations between the three variables were positive and highly significant. Figure 5.1 shows the relationship between mandible length and the two other characters in 21 caterpillars of 9 species from 3 families. Due to their relative hardness, caterpillar mandibles readily survive passage through the chick's gut and may easily be dissected out from faecal sacs and measured under a dissecting microscope. The strong correlation between mandible length and body size across many caterpillar taxa allowed a prey size distribution to be estimated from caterpillar mandibles alone without the need to identify the species from which they came.

Table 5.1. Intercorrelations among measurements of caterpillars of nine species from three families.

	Head width	Total length.
Mandible length	0.902 P<0.001	0.817 P<0.001
Head width	-	0.779 P<0.001

In the laboratory, each faecal sac was dissected in a Petri dish of 20% ethanol. The dish was systematically seached for mandibles under both high and low magnifications. Mandibles could be identified as of Geometrid, Noctuid or Tortricid type (which differ markedly) by comparison with the identified specimens. Within each type, mandibles from a particular sac were

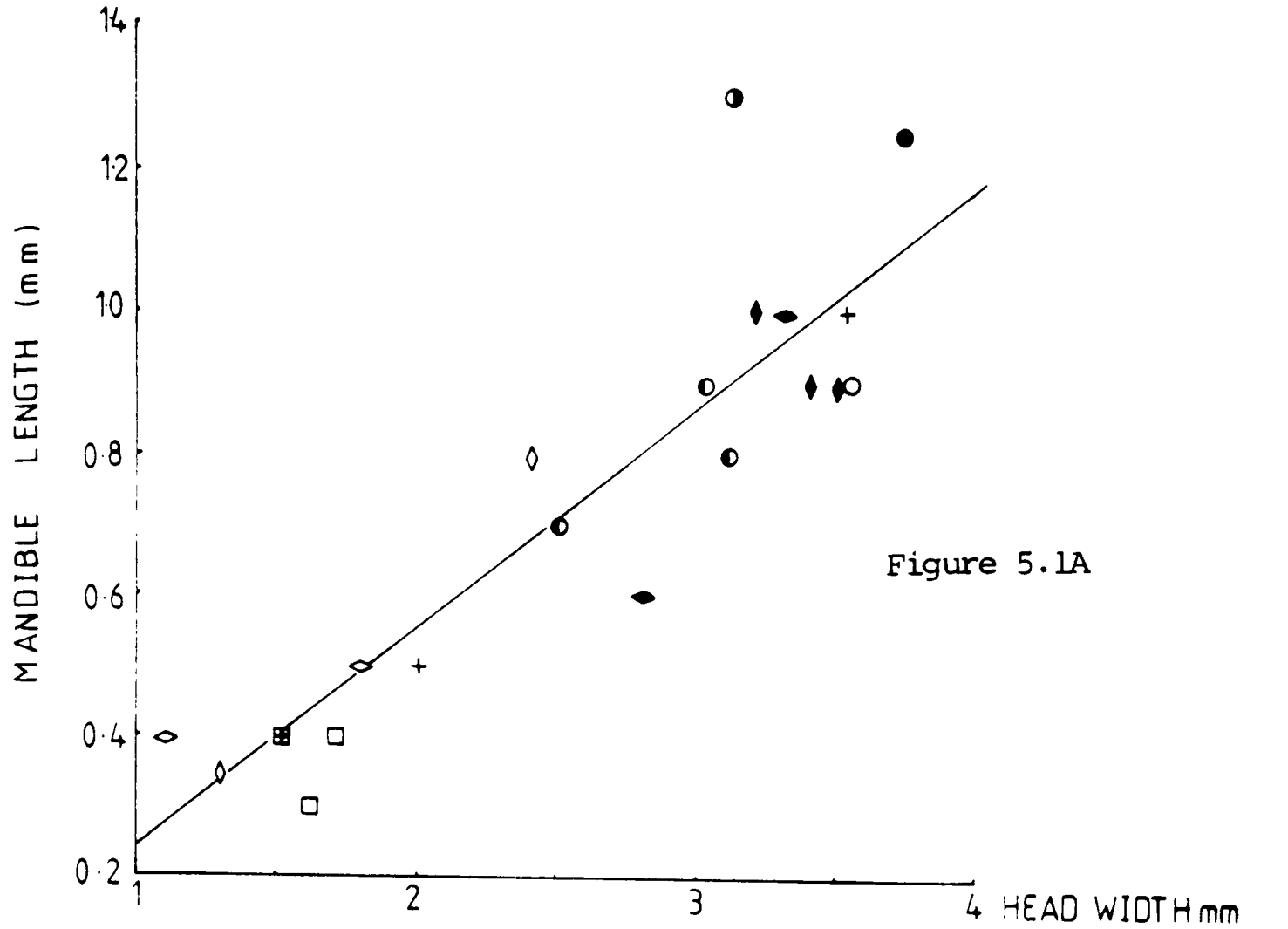


Figure 5.1A

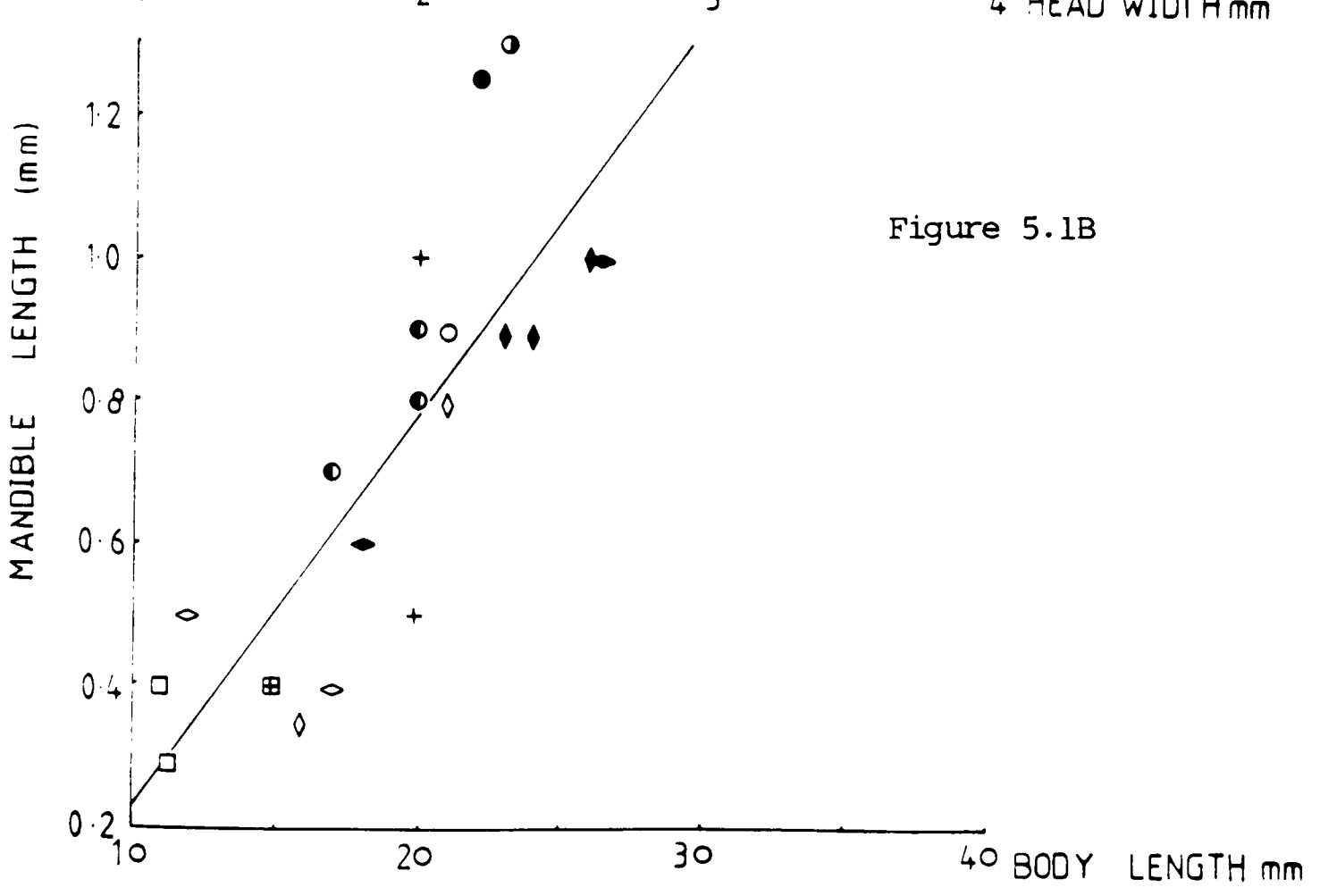


Figure 5.1B

Figure 5.1. The relationship between mandible length and head capsule width (5.1A), and total body length (5.1B) across nine species of caterpillar taken by Great tits during the summer of 1984. The symbols used are as follows: GEOMETRIDAE (diamonds): **Agriopys sp.** ◊ , **Erranis defoliaria** ◆ , **Colotois pennaria** ⧫ , **Operophtera brumata** ◇ .NOCTUIDAE (circles): **Amphypyra berbera** ○ , **Drybotodes sp.** ◐ , **Orthosia stabilis** ◑ , **Griposia apulina** ● .TORTRICIDAE (square): **Tortrix viridana** □ , Unidentified: + .

paired by size and colour, so that the number and size of prey items rather than of mandibles could be determined. Hence data collected from faecal sacs were minimum estimates of prey number per sac. In addition, the abundance of caterpillar spiracles (which were also well preserved in samples) was scored on a scale of 0 - 5 as below. This gave an estimate of the number of caterpillars represented in the sample which was independent of the number of mandibles. Although caterpillars formed the bulk of prey remains in faecal sacs, the presence of other invertebrate taxa was recorded and an estimate of the total number of non-caterpillar items present was recorded as follows:

0 none (this category was never recorded)

1 1 - 10 items

2 11 - 25 items

3 26 - 50 items

4 51 - 100 items

5 >100 items

assessed in this way, estimates of non-caterpillar prey (NCP) between nests were normally distributed. Data collected by faecal analysis may be biassed in a number of ways, especially in relation to variation in prey handling between birds. In the case of caterpillar mandibles, any systematic tendency by a bird to remove the heads of caterpillars, especially of larger prey which may be harmful to young chicks (Perrins 1979) would bias estimates of prey size in favour of smaller items. However, the correlation between the minimum number of caterpillars in the sample and the estimated number of spiracles was positive and highly significant (r_{83}=0.709 P<0.001, for data from both years combined) suggesting strongly that no systematic bias was present.

Only prey distributions based on more than 6 caterpillars were used in the analyses since smaller samples would be inadequate to determine prey size variation. Since small samples were often involved in estimates of prey size variation, standard parametric measures of variation (such as variance or standard deviation) could not be used as they are markedly influenced by outlying variates in small samples. Instead, the Shannon-Weaver diversity statistic $\bar{H}$ was used. This was calculated as:

$$\bar{H} = \quad p_i . \mathrm{Log}_e p_i$$

(MacArthur & Wilson 1967).

where p_i is the probability of a mandible falling into the ith size class. This statistic is uninfluenced by outlyers as it measures the number of size classes in the distribution, rather than the spread of those classes (see Tramar (1969) for a detailed account of the properties of the $\bar{H}$ statistic). It is, therefore, the diversity of caterpillar prey sizes that was estimated. Since the statistic is influenced by the number of prey items found in a sample, it was standardised by removing the variance due to sample size in a linear regression analysis.

5.2.2 Results.

Table 5.2 shows sample statistics for caterpillar prey size determined from nestling faecal analyses over two summers. About half of the samples were rejected for further analysis as they contained the remains of fewer than 6 caterpillars. Thus for the two years combined, samples from 40 broods were suitable for analysis.

If bill length and prey size were correlated, the value of $\bar{H}$ must increase with increasing parent bill difference. However, $\bar{H}$ will asymptote when the bill lengths are so different that there is no overlap in their associated prey size distributions. Appendix 5 is a model deriving this theoretical maximum $\bar{H}$ or asymptotic value. A theoretical value of 1.83 was obtained. Figure 5.2 shows the relationship between prey size diversity and the difference in parent bill lengths in 1984. Prey size diversity increased along a decelerating curve asymptoting at an $\bar{H}$ value of about 1.8. This was close to the theoretical value of 1.83. This relationship explained 68% of the variance in prey size diversity. Since neither variable correlated significantly with date, brood size, NCP score, or the mean prey size, this may be accepted as an unconfounded relationship. In 1984, eight nests were available where either the parents differed by less than 0.2mm in bill length, or there was only one parent present. Figure 5.3 shows the relationship between mean prey size and mean bill length at these nests. The correlation was significant and negative, indicating that longer-billed birds tended to take significantly smaller prey. In 1985 there was no significant correlation between prey size diversity and bill length difference (r_{16}=0.092). Nor was there any correlation between mean bill length and prey size at nests with

Table 5.2. Prey sample statistics determined from chick faecal analysis.

* sub-sample with more than 6 caterpillars per brood sample.

	1984	1985	'84/'85 combined.
No. faecal sacs.	89	73	162
No. broods.	51	32	83
No. mandibles.	356	346	7Ø2
No. caterpillars.	265	23Ø	495
Mean mandible size ± 1sd.	Ø.78±Ø.27	Ø.75±Ø.19	
Mean non-lep. prey score (NCP)	3.17±1.41	2.16±1.3Ø	
No. brood samples with >6 caterpillars	22	18	4Ø
Mean mandible size ±1sd of prey in sample used.	Ø.75±Ø.16	Ø.76±Ø.14	*
No. caterpillars in sample used	2Ø7	194	*
Mean non-lep. (NCP) score of samples used.	3.45±1.3Ø	2.39±1.24	*

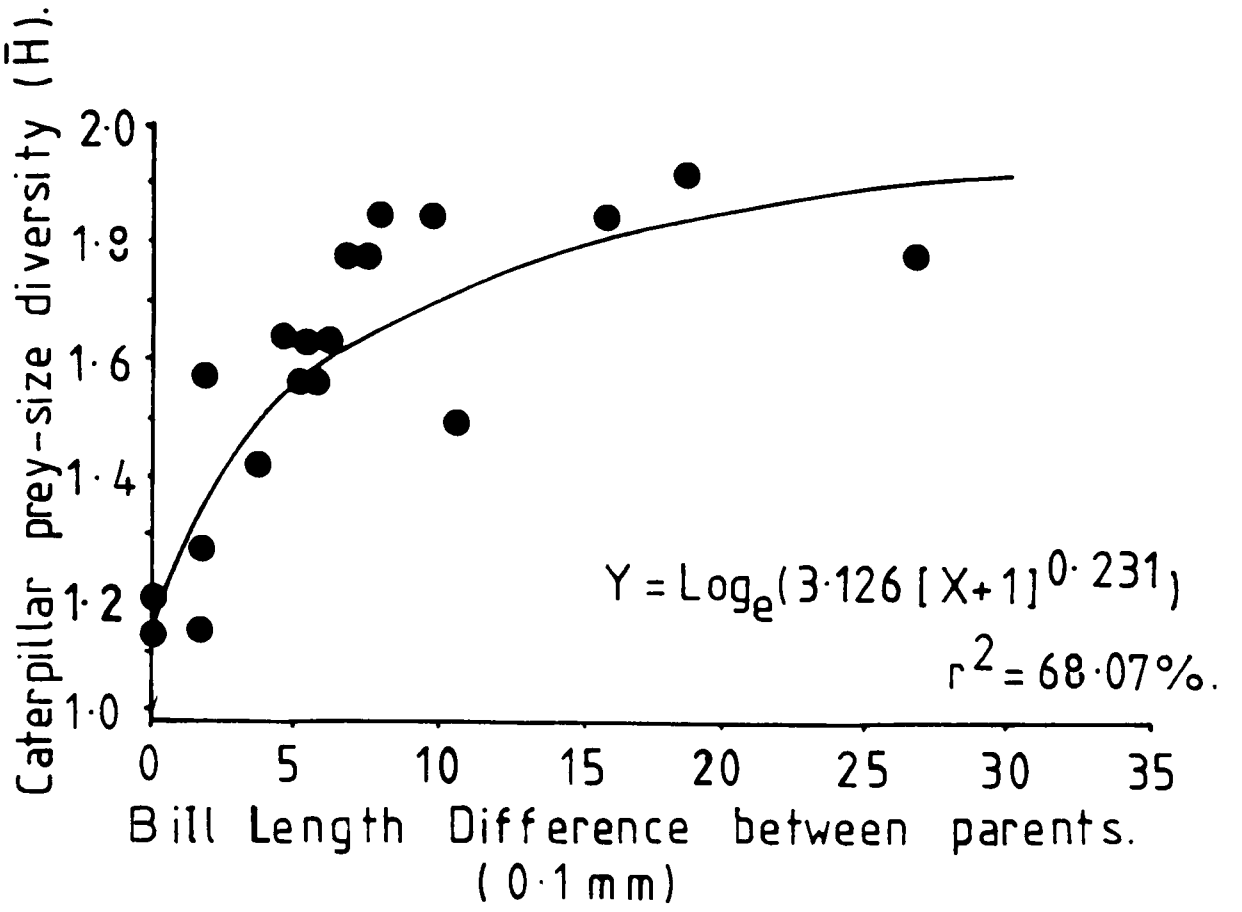


Figure 5.2. The relationship between the diversity in prey size brought to the nest and the difference in the parents bill lengths across 22 broods sampled in 1984. The prey size diversity was standardised relative to the mandible sample size available for each nest. The curve fitted agrees closely with a model (Appendix 5) based on a prey distribution associated with each parent's bill length - see text.

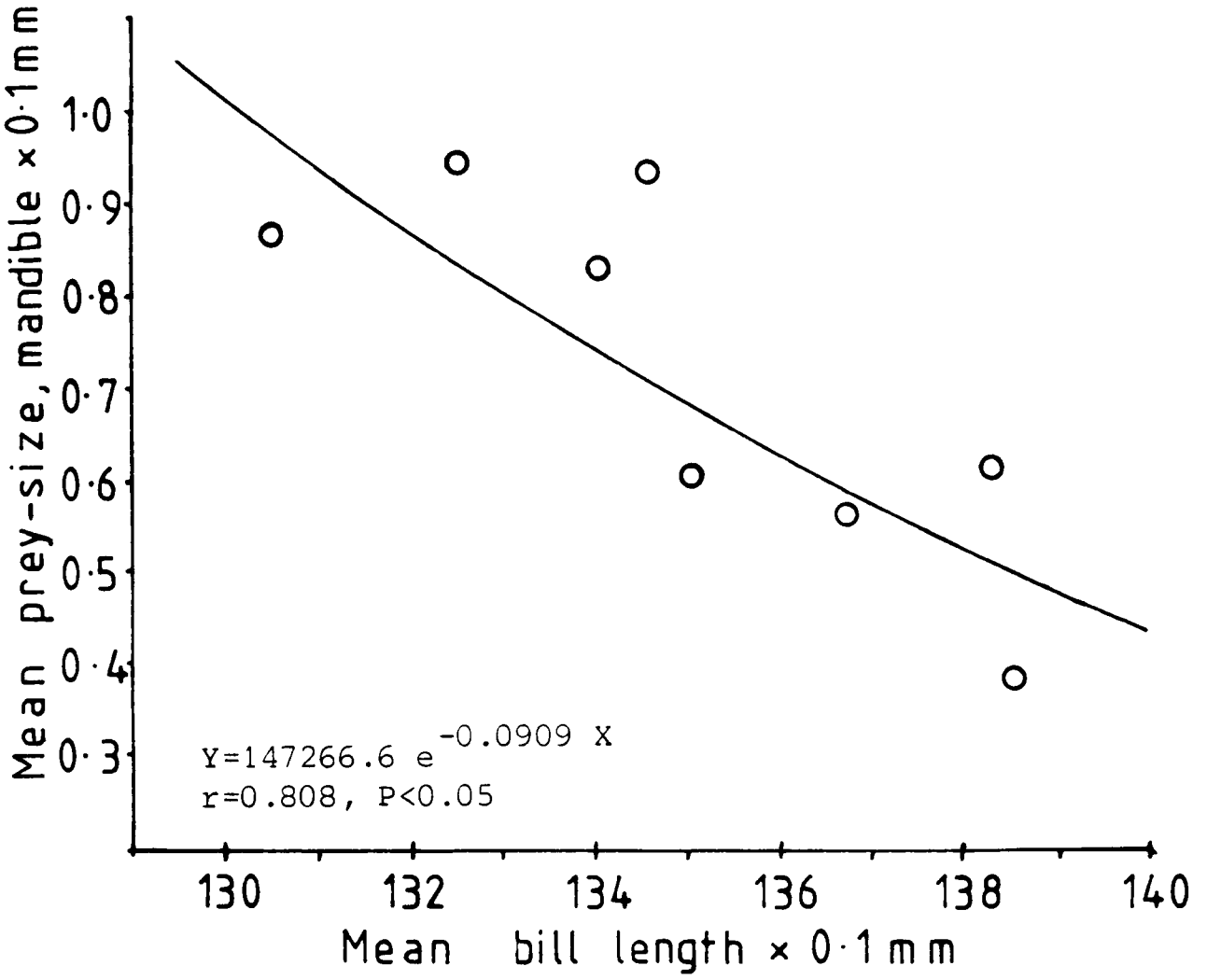


Figure 5.3. The relationship between mean prey size (given as prey mandible length) delivered to the nest and the mean bill length of the parents. Data are from eight nests in 1984 for which the parents shared the same bill length - see text.

similar or single parents (r_6=0.04). This dramatic difference between years suggests that whilst in 1984 birds foraged selectively relative to bill length, in 1985 they did not. The implications of this are considered below.

In 1985, faeces from only 14 adults were available for analysis. The number of caterpillars represented in each sample was very low with a mean of 1.83±1.02. This sample was too small to determine the mean prey size per bird so that a direct comparison of individual prey size and bill length was not possible. However, the mean prey size for the 21 caterpillars available from the 12 birds (represented in Fig 5.2) of 0.557±0.26 mm was lower than that fed to chicks (Table 5.2), and the score of non-caterpillar prey was significantly higher (3.27±1.53) than that fed to chicks (t_{44}=2.37, P<0.05, two-tailed test), suggesting that the parents took a wider range of generally poorer quality food than they fed to the chicks.

5.2.3 Discussion.

The analyses presented above suggested strongly that parental foraging was more diversified than might be indicated by the prey brought to the nest. In 1984 there was strong evidence for a correlation between prey size and bill length and this was negative. In 1985, prey size varied randomly with respect to bill length. The two summers differed markedly in weather conditions as shown in Table 5.3. The difference between the two years is adequately summarised by a statement from the Radcliffe Meteorological Observatory, Oxford:

"After two warm, dry summers in succession 1985 gave us a summer notably cooler and wetter than average. This poor summer...(was)...the seventh wettest June on record at Oxford and the eighth coldest..." C.G.Smith (1986).

Following Schoener's (1971) model, when food is abundant birds should forage selectively. When scarce, their foraging should be more general. Hence the presence or absence of a relationship between bill length and prey size apparently seen in these data might be explained if food had been significantly more abundant in 1984 than 1985. Although the weather was generally poorer and mean chick weights were significantly lower in 1985 than 1984, the mean brood size was larger in 1985 and the total net weight of chicks fledged per brood was higher. Therefore although one might have expected foraging conditions to have been poorer in 1985, there is little evidence for this from the condition of chicks. Indeed, in this study area eleven (12.5%) Great tit nests failed after hatching in 1984 whilst eight (12.6%) failed in

Table 5.3 Weather conditions and breeding success in Extra, Common Piece and Great Wood in 1984 and 1985. Meteorological data are from the Monthly Weather Report of the Meteorological Office.

(a) Weather. Temperatures in celsius, rainfall in mm.

	Min. Temperature	Max. Temperature	Mean	diff from 30 yr mean	total rain	% of 30 year mean.
May 1984	6.0	14.5	10.3	-1.6	72	136%
June 1984	10.8	20.8	15.8	+0.8	30	51%
May 1985	7.3	15.7	11.5	-0.4	81	152%
June 1985	9.0	17.5	13.3	-1.7	123	208%

Summaries:

May 1984 "Mostly dry and sunny in north, dull and wet in south."
June 1984 "Mostly dry and sunny, thundery at times."
May 1985 "Mainly dull andy rather wet."
June 1985 "Generally cold and wet."

(b) Breeding success. t values are given for comparisons between years.

	1984 (n=76)	1985 (n=56)	t	P
Mean 15th day date.	43.5±6.2	32.2±4.2	12.43	<0.001
Mean chick weight.	19.0±0.9	18.5±1.4	2.34	<0.05
Mean brood size.	7.4±2.0	8.6±1.8	-3.67	<0.001
Mean total brood wt.	140.6±38.0	159.8±33.8	-3.05	<0.01
Mean female fat*.	2.2±0.7 n=82	1.7±0.8 n=62	3.75	<0.001

* No significant differences were found in the mean weight or tarsus lengths of males or females between years, nor was there a significant difference in the mean fat score of males.

1985. Hence in the absence of data on caterpillar abundance in the two years, the results are suggestive, but inconclusive.

5.3 Bill size in relation to breeding success.

The probability of survival for Great Tits during the first few months after fledging is strongly correlated with their weight at 15 days of age (Perrins 1963). Many factors contribute to the variation in this weight among chicks. Brood size, and fledging date both correlate negatively with fledgling weight (Perrins 1963, 1976), (although all of the variation in chick weight due to date in the present data could be accounted for by variation in the NCP score - section 3.5.1) and the mean parent weight correlates positively (a component of fledging weight which may be partly genetic and/or is correlated with parental and/or territory quality) (Van Noordwijk 1984). If the difference in the parent bill lengths contributed to the variation in chick fledging weight, selection might operate to maintain a difference in parent bill lengths.

To investigate this further, the mean weight of chicks per brood was entered as the criterion variable in a stepwise multiple regression analysis with brood size, mean parent weight, 15th day date, caterpillar prey size diversity and the NCP score as predictor variables. The analyses were carried out on the data for the two years (1984 and 1985) separately. In 1984, only the difference in parent bills and the amount of non-caterpillar prey were significant determinants of chick weight. Bill difference explained 25.39% of the partialised variance in chick weight, and NCP - a further 19.83%. Figure 5.4 shows the relationship between fledging weight and the difference in parent bill length for the 22 broods analysed in 1984. Caterpillar size diversity contributed less than 1% to the variance in chick weight. In 1985 none of the variables explained a significant part of the variance in chick weight.

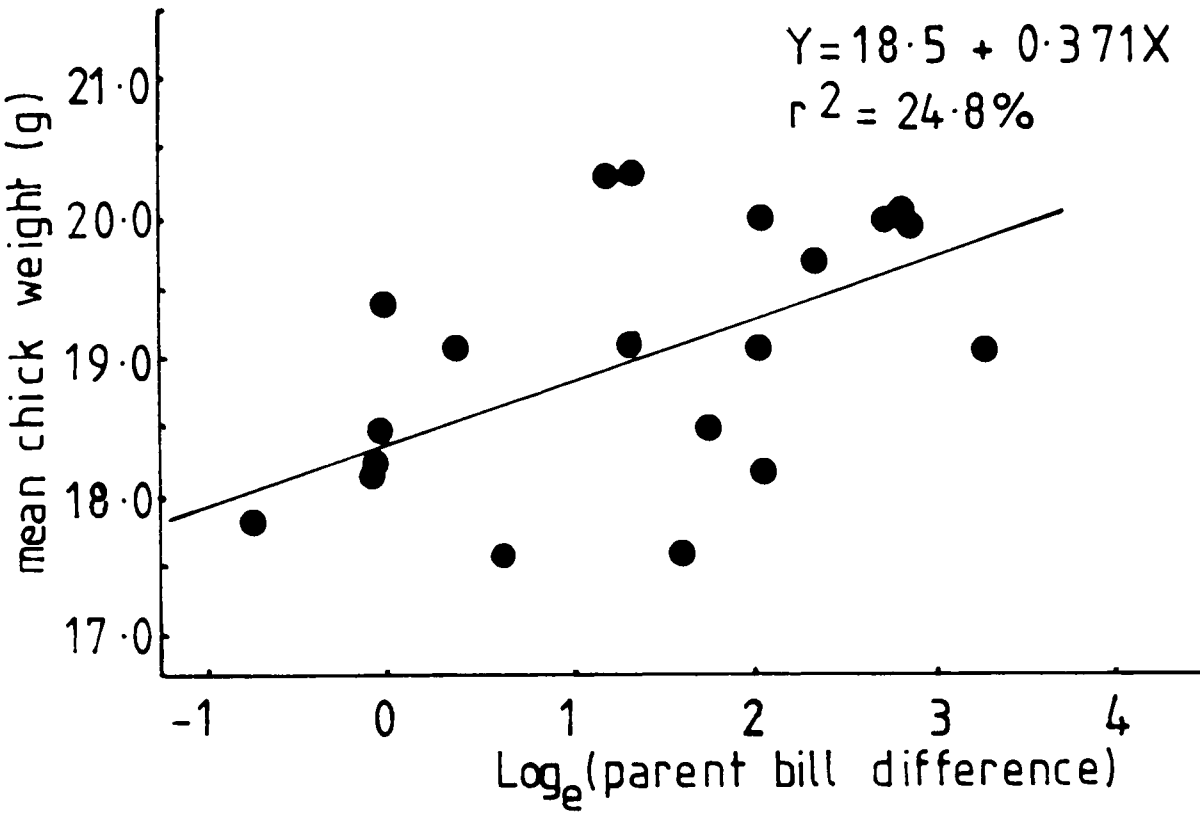
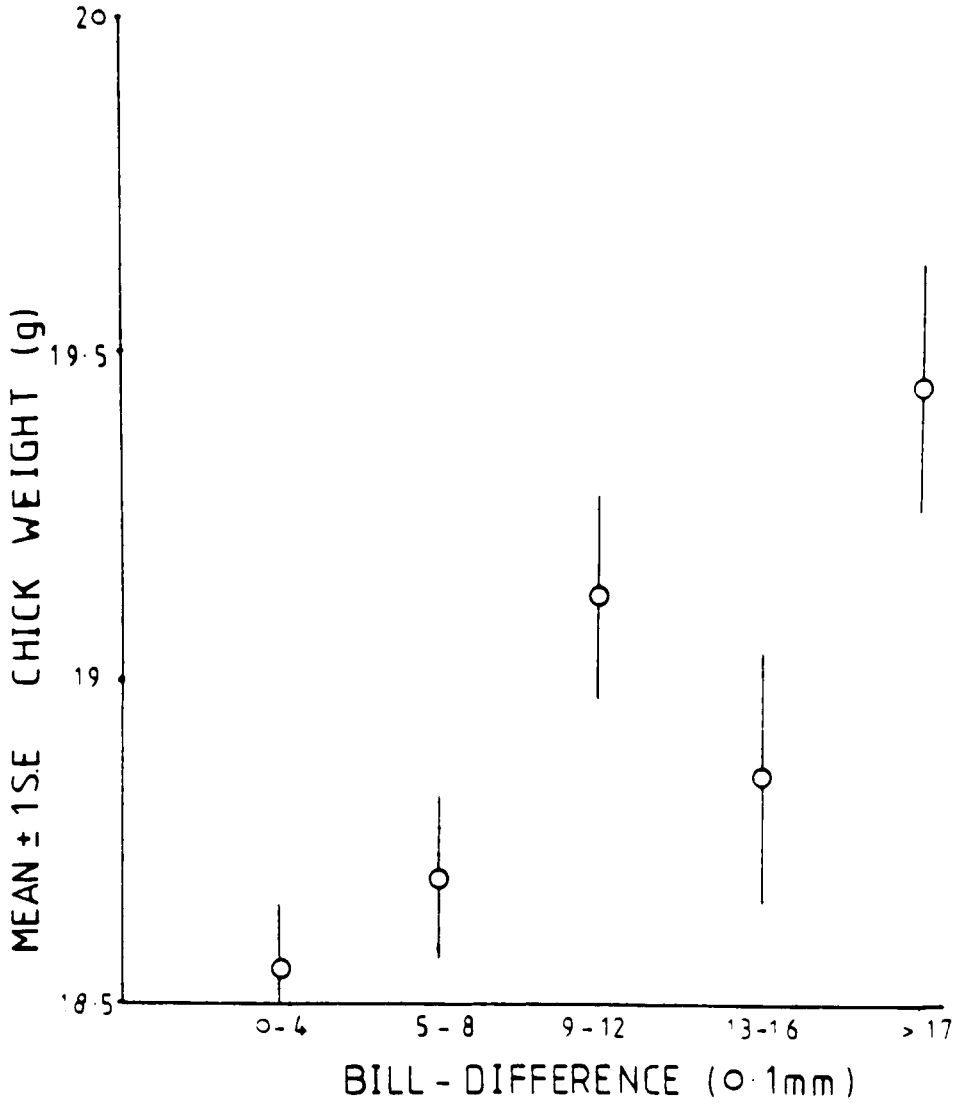


Figure 5.4. The relationship between the mean chick weight (day 15) per brood and the difference in the parent bill lengths for 22 nests sampled in 1984. The regression line fitted was statistically significant ($F_{1,20}$=5.61, P<Ø.Ø5).

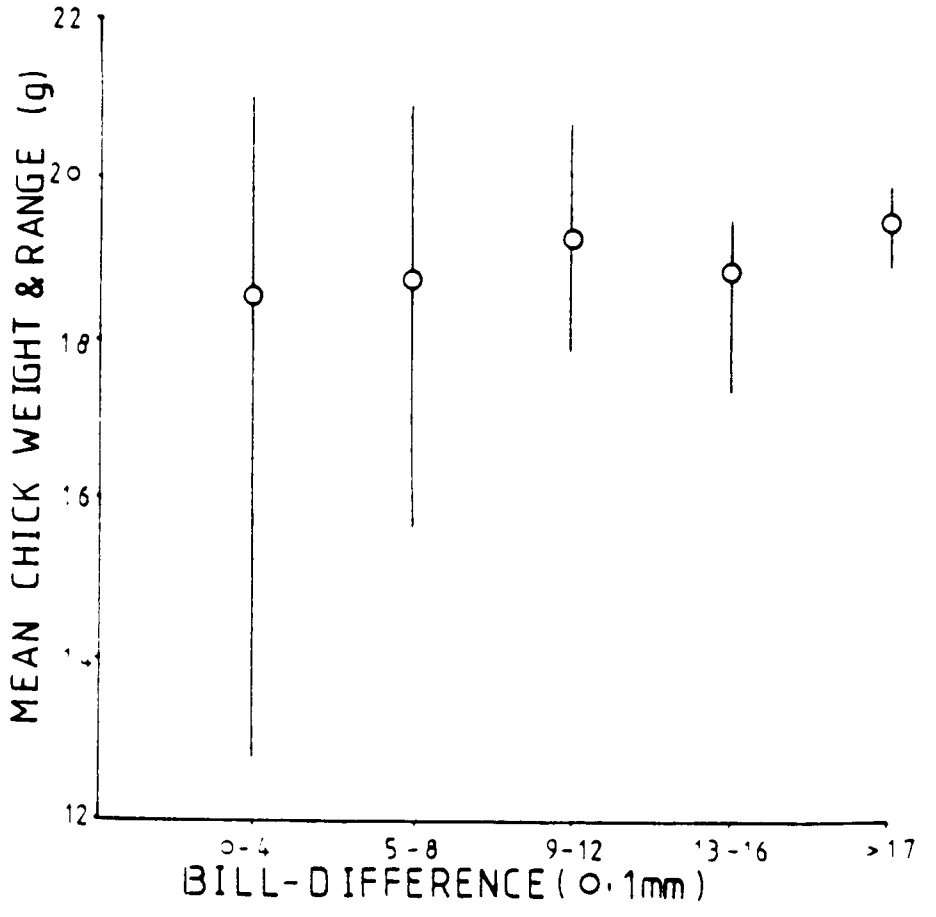
To increase the sample size, I repeated this analysis on mean chick weights for all nests where the bill length difference was known for the parents in the four years 1982-1985, a total of 286 nests. To remove between-year variation, variables were expressed as deviations from the yearly mean. Mean chick weight was again entered as the criterion variable in a stepwise multiple regression analysis with mean parent weight, date, brood size and bill-difference as predictor variables. Chick weight was transformed to normality by taking the exponent value, date and bill-difference by taking the natural logarithm. Brood size, parent weight and bill-difference all contributed significantly to the variation in chick fledging weight although together they explained less than 7% of the variation. Table 5.4 gives the partial correlation coefficients for chick weight and the three significant correlates.

Figure 5.5a shows the mean chick fledging weight in relation to the difference in bill length (grouped into discrete classes) for the 286 broods. Figure 5.5b shows the range in fledging weight associated with each bill-difference size class. From this it is clear that although the majority of broods reared by parents of equal bill length were of average weight, all of the light broods came from nests in which the parents were very similar in bill length. The bill-difference was significantly lower at nests where the mean chick weight was more than one standard deviation below the mean weight of 18.6$\pm$1.15g for the population (Mann-Whitney U test, P=0.005).

There is some evidence that a difference in parental bill lengths may be beneficial to the survival of fledged young since there is a tendency for parents with different bill lengths to raise heavier chicks. To assess the relationship between fledging weight and survivorship during the period



5.5A



5.5B

Figure 5.5A. The mean ± 1 s.e. of chick weight (day 15) per brood in relation to the difference in the parent's bill lengths across 286 nests from four summers (1982-1985). Data were standardised to remove between-year differences in the mean chick weights. 5.5B. shows the mean and range of the same data showing that light broods tended to come from nests where the parents had more similar bills than the average.

Table 5.4 Partial correlation coefficients between the exponent of chick 15th day weight and each of 3 significant correlates for 286 broods. Data are for the years 1982-1985.

Variable	Partial correlation coefficient.	
Brood Size	Ø.194	P<Ø.Ø1
Mean Parent Weight	Ø.123	P<Ø.Ø5
Parent Bill difference	Ø.121	P<Ø.Ø5

1982-1985, I have calculated the % of chicks from a weight class that were known to be alive at least 3 months after fledging. Figure 5.6 shows this relationship. Table 5.5 shows the number of broods falling into each mean weight and bill-difference class. When these figures are multiplied by the appropriate probability of survival shown in Figure 5.6 an estimate of the number of broods in each weight and parental bill-difference class surviving to 3 months is obtained. If summed across weight classes within a bill-difference class an estimate of the number of broods in each bill-difference class surviving 3 months is obtained. This may then be expressed as a % of the original number of broods in each class to obtain an estimate of the relative fitness of each bill-difference class. This is summarised in Table 5.6.

This shows that a slight advantage is gained by a bill difference of 0.9-1.2mm and that on average some 4% fewer chicks were recruited into the population from parents with more similar bill lengths. Although not a large difference, if this pattern of survival occured over many generations it might be sufficient to maintain sexual dimorphism in the population by natural selection against chicks from similarly-billed parents.

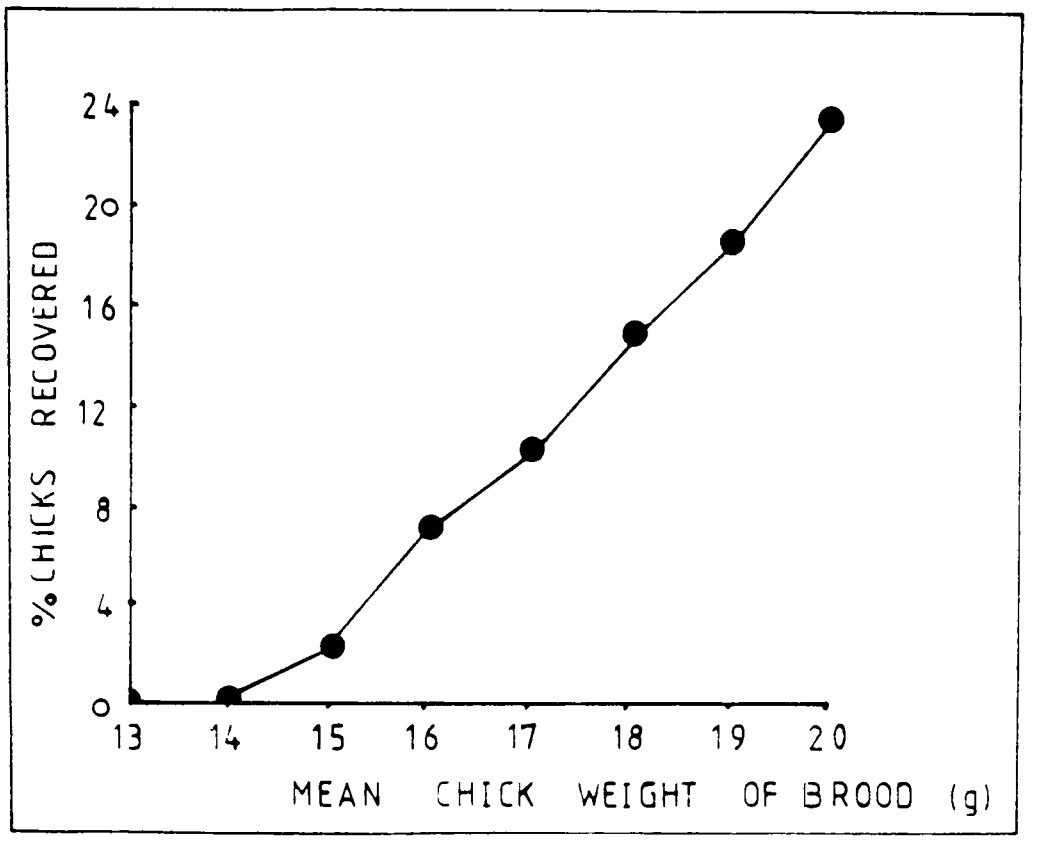


Figure 5.6. The relationship between the recapture probability of fledgling Great tits and the mean chick weight of the brood from which they came. Data from four summers (1982-1985) are pooled in this figure.

Table 5.5. Observed numbers of broods falling into each weight and parental bill-difference class.

Wt(g)	13	14	15	16	17	18	19	2Ø	21	Total
Bill diff (Ø.1mm)										
Ø-4	1	1	1	4	18	44	51	29	4	153
5-8				2	5	26	27	15	3	78
9-12						7	8	11	1	27
13-16			1				7	2		1Ø
17+							4	2		6

Table 5.6. Estimating the relative fitness of bill-difference categories.

Bill-difference class (Ø.1mm)	Number broods fledged	Estimated number surviving 3 months	% surviving.
Ø-4	153	28.46	18.6
5-8 (observed mean)	78	15.79	2Ø.2
9-12	27	6.Ø5	22.4
13-16	1Ø	1.81	18.1
17+	6	1.18	19.6

5.4 Bill size and mate choice.

The difference in the parent bill lengths is not a major contributor to chick survival. The high correlation between this variable and chick weight found in the 1984 sub-sample partly reflects the removal of other causes of brood loss from the sample analysed. For example, the sample was biassed by being taken from broods that survived to day 15. Under more natural circumstances, brood loss due to predation before this age may be very high (Dunn 1977). Hence mate selection should be expected on many criteria other than bill size. To test for assortative mating on the basis of bill length, I calculated the correlation between bill lengths of paired males and females in each summer. The correlations among paired individuals and the mean $\pm$ 1sd absolute bill length difference in each summer are shown in Table 5.7 below. If the birds paired in such a way as to maximise the difference in bill length, a negative correlation should be expected.

In each year the correlation was positive, and in three summers, the correlation was not statistically significant. In 1983 however, there was a significant positive correlation. Such a correlation could occur through a relationship between bill length and habitat (Snow 1953) since the sexes share a common environment. The effect of habitat on bill length in summer is discussed further in chapter 6. Since none of the correlations was negative, the analyses provide no evidence for assortative mating to maximise the bill-difference.

Table 5.7 Correlations between bill length within pairs of breeding Great tits in 1982-1985. the mean observed and expected differences between partners are given together with the t values for comparisons of these.

Year	n.	Correlation between sexes.		Absolute diff.
1982	59	Ø.165	NS.	5.46±4.Ø9
1983	1Ø3	Ø.3ØØ	P<Ø.Ø1	4.38±3.Ø4
1984	8Ø	Ø.1ØØ	NS	6.28±5.2Ø
1985	6Ø	Ø.226	NS	4.1Ø±3.2Ø

5.5 Discussion.

The hypothesis that selection for sexual dimorphism in bill length might come about through the differential survival of offspring in itself does not predict that females should be longer-billed than males. Indeed, if bill-difference is expressed as (x_{mother}-x_{father} no significant explanation of the chick weight occurs. Hence it seems unimportant to the chicks that the mother's bill should exceed the father's, only that the sexes should differ. Because of this, and because it ignores other possible constraints on bill length, this approach cannot be used to predict what will be the expected mean bill lengths of the two sexes in the population. Although the 'optimum' bill length difference predicted from Table 5.6 was 0.9-1.2 mm, the mean observed differences were always less than this (Table 5.7). This would be expected if a structural constraint (such as jugal length) were imposed on the maximum bill length.

It is not clear how a relationship between parental bill-difference and chick fledging weight might operate. Since there was no correlation between the variation in prey size brought to the nest and the fledging weight of chicks, it is unlikely that the relationship acts directly through the mediary of prey size. A more reasonable hypothesis is that in selecting prey of slightly different sizes, partners of different bill sizes compete less for food within the territory than parents of similar bill size. Tinbergen (1960) showed that Great tit partners often foraged together, and that the type of prey taken by one partner was (to some extent) influenced by that taken by the other. Competing parents would be expected to have a lower rate of provisioning to the nest and so the weight of chicks would be lower.

I have provided some evidence that the contents of nestling faeces may give

a poor indication of the prey taken by the parents for their own consumption. Since bill variation in summer is determined largely by factors acting within that season (both genetic and environmental) an alternative (or additional) explanation for sexual dimorphism in bill length might be sought in terms of direct competition between the parents.

Sexual dimorphism in summer might represent 'character displacement by underutilisation'(Hespenheide 1973 - see chapter 1). For this to occur, the sex difference must itself be genetically determined. If not, 'hybridisation' between the sexes would prevent character displacement. It is difficult to see how this might have arisen if bill length and prey size were negatively correlated since each sex would need to become more like the other to exploit an underutilised part of the resource curve at its 'end' of the resource gradient. However, if true, it might explain why females were longer-billed than males, since the process emphasises existing variation. In this case, females would be longer-billed because of niche segregation in winter.

Hence, in conclusion, whilst there is some evidence for a selective cause for sex differences in bill length in the summer acting through the differential survival of offspring, it is unlikely that this solution represents the whole story.

Chapter 6. The relationship between bill size and habitat in summer.

Chapter 6. The relationship between bill size and habitat in summer.

6.1 Introduction.

I have shown that bill length and prey size may be correlated in breeding Great tits, and that this may have a small but significant effect on chick fledging weight, and subsequently survival. Further, bill length varied less between summers than between summer and winter, and I suggested that this may reflect either a reduced environmental component of phenotypic variation in summer, or that different environmental factors influenced bill size in summer and winter. Observations on bill moult suggested that there may be a behavioural component in the determination of bill size in summer. That there is a significant environmental component to variation acting within the season of observation, implies that bill variation and/or changes in the bill should correspond to variation in the habitat or in habitat use (niche).

Previous work on bill variation in relation to broad differences in habitat type was discussed in chapter 1. In chapter 2, I pointed out that coniferous woodland occurs only in relatively small (and usually mixed) stands at Wytham, hence I shall not explore further the relationship between bill size and woodland type described by Snow (1953). This chapter attempts to relate bill variation specifically to habitat in the breeding season.

The study of habitat use in relation to morphology is particularly difficult in a mobile animal. The home range of the Great tit may cover many hectares (Perrins 1979 and figure 2.8), so that it is only during the breeding season that variation among individuals may be related to that of habitat (as opposed to niche) in any detail. When the characters under study are

phenotypically plastic, two approaches to this problem may be used in the study of a wild population. First, the same genotype may be observed in different habitats between years (longitudinal study). This is an indirect method (because a relationship cannot be inferred from observations made in a single season) in which between-year effects must be considered. Secondly, morphological variation may be examined among habitat types within years (cross-sectional study). This is a direct method in which other causes of variation (age, body size etc) must be taken into account. When a control group is available (eg: birds remaining in the same habitat between years), the indirect approach gives the greatest indication of a habitat effect. However, neither method defines precisely which environmental component(s) may be responsible. Both methods will be used here.

6.2 Methods.

The analysis of habitat poses considerable problems in ecology (Elton 1966, Gauch 1982). In ecomorphological studies, the most complex multivariate analysis may fail to construct a realistic habitat classification (that is, one that covaries with patterns of morphological variation) simply because, whilst adequately summarising the environmental variation present, it may fail to identify or weight sufficiently those features of the habitat that are of greatest significance to the species concerned. This is partly a problem of analytical resolution and sampling. For example, consider a single classification ANOVA in which variation in a quantitative trait is examined with habitat types as the treatments (eg: Boag and Grant 1978). If the sampling area is resolved into too many habitat types (relative to the distribution and density of animals) samples may be too small in each habitat to recognise an effect (Type 2 error). If too few habitats are resolved, real variation may become 'pooled' within habitats and again one may fail to observe an effect.

Alternatively, the habitat classification might be based on some attribute of the birds themselves. For example, by identifying areas of high or low breeding success (Perrins 1963, Krebs 1970). From this, one may work back to the habitat matrix, so defining which environmental components contribute most to differences among 'good' or 'bad' habitats. However, this *a posteriori* method is invalid in any further analysis of morphology, as it risks confounding the morphological variation among habitats if morphology and breeding success are themselves correlated. In the study of qualitative traits it has been possible to define geographical areas which differ significantly in character composition on the basis of that character

composition itself (Holloway 1969, Adams 1974). However, this is more difficult with quantitative traits as character states are less easily defined.

A habitat type contains many strongly associated features (or components). That is, one might recognise a habitat type by the greater association of habitat components within than between habitat types. This, apparently circular reasoning, provides an objective method to test the validity of habitat types which have been defined subjectively. For present purposes, a habitat classification is required only to summarise the pattern of association between habitat components. The present analyses are essentially a priori, that is, the classification of habitat preceeded the analysis of its association with Great tit morphology. However, some 'key' habitat components which are believed to be of importance to the Great tit have been used to classify habitats.

6.2.1 Direct methods of assessment.

6.2.1a The classification of habitat.

To relate bill variation to habitat at Wytham, a habitat classification (a priori) was required. For this purpose, the 100m National Grid (already laid out at Wytham) was used as a sampling grid. Bill variation among breeding adults was related to this grid through the nestbox location. However, since a Great tit territory is itself approximately 1ha in area (Krebs 1971), I blocked grid squares into 4ha units or tetrads. This gave 49 tetrads with a mean of six nestboxes per tetrad. Figure 6.1 shows the tetrad map of the study area. Within each tetrad, the presence or absence of 24 habitat components was recorded. These were based on those of Fuller (1982) but recorded more tree and shrub species. The components used were:

1 Broad-leaved woodland	13 Grassland
2 Coppice	14 Ditch < 5m width (wet)
3 Sycamore as a standard *	15 Grazing
4 Oak as a standard	16 Hedge with mature trees
5 Ash as a standard	17 Hedge without mature trees
6 Beech as a standard *	18 Parkland
7 Even-aged conifer plant.*	19 Blackthorn thicket
8 Un-even aged conif. plant.	20 Elder
9 Mixed woodland	21 Maple as a standard *
10 Pioneer scrub*	22 Beech Plantation
11 Carr	23 Nettle as a dominant herb
12 Even-aged decid. plant.	24 Ferns as a dominant herb.

* 'Key' components.

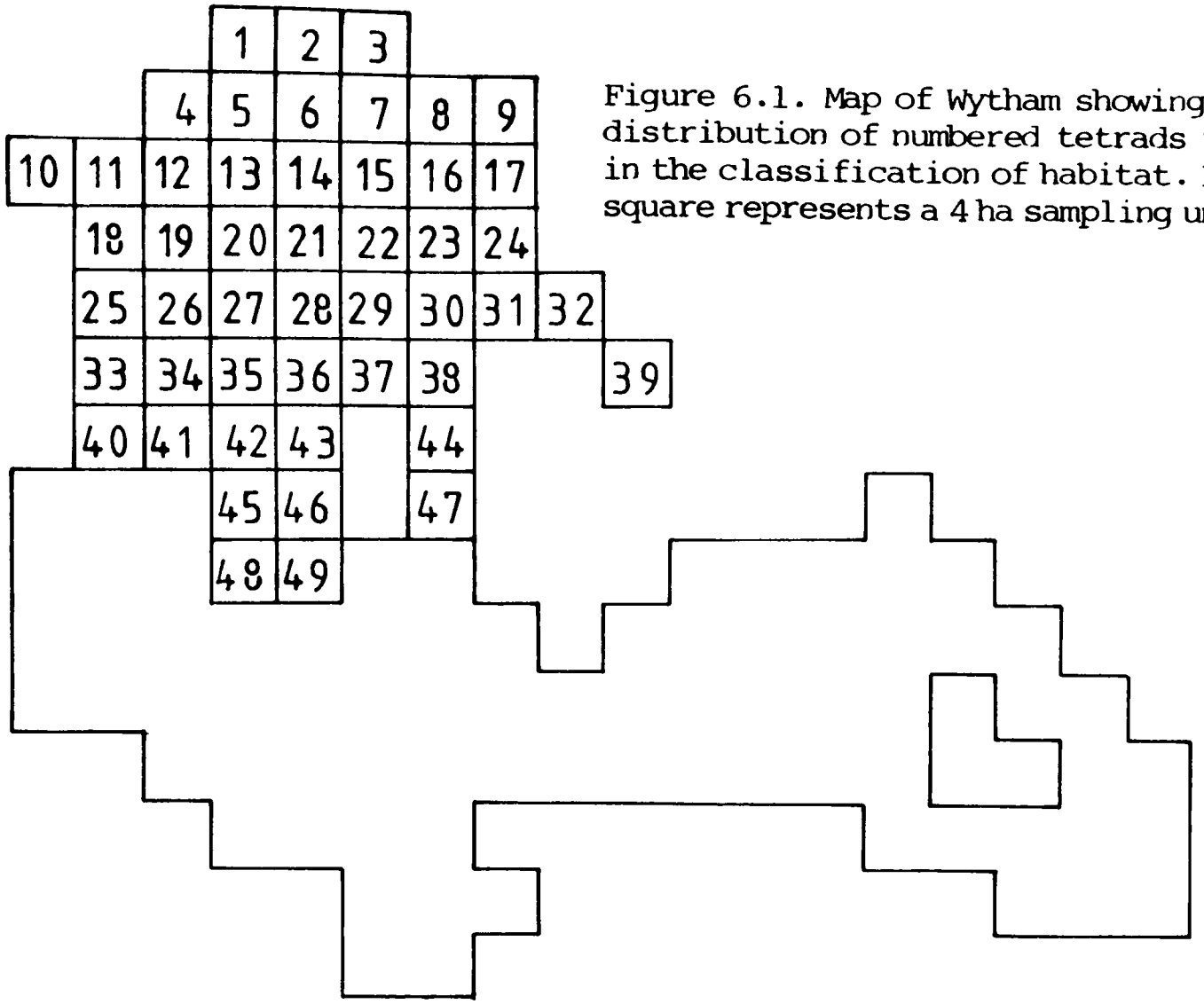


Figure 6.1. Map of Wytham showing the distribution of numbered tetrads used in the classification of habitat. Each square represents a 4 ha sampling unit.

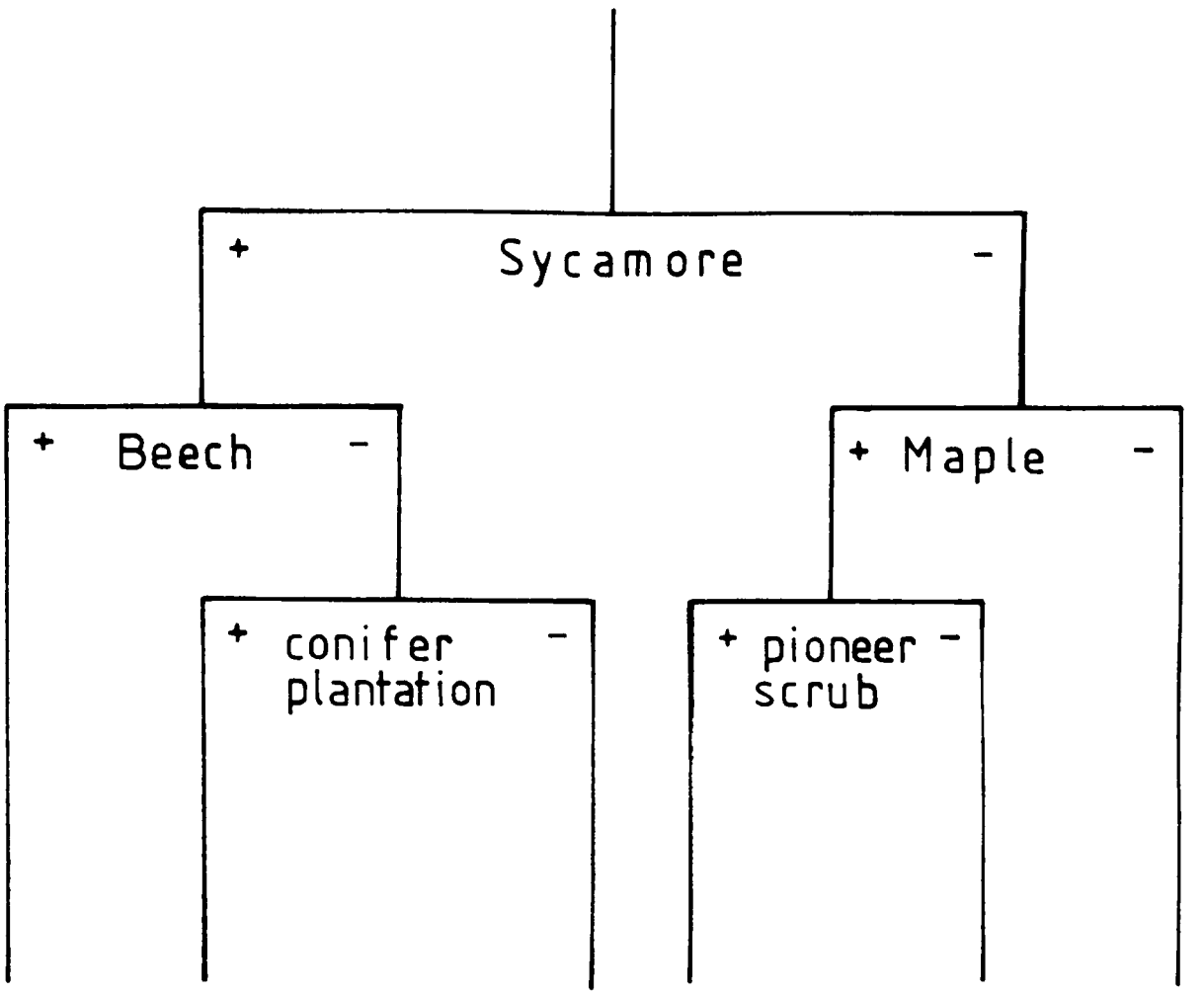
Table 6.1. Habitat matrix. Tetrads grouped by habitats.

		HABITAT COMPONENTS																							
		1				5					10					15					20				24
	35	1	1	1	1	1	1	0	0	0	1	0	1	0	1	0	0	0	0	0	1	0	0	0	0
	36	1	1	1	1	1	1	0	0	0	1	0	0	0	1	0	0	0	0	0	1	1	0	1	0
	37	1	1	1	1	1	1	0	0	0	1	0	0	0	0	0	0	0	0	0	1	1	0	1	1
	38	1	0	1	1	1	1	0	0	0	1	0	0	1	0	0	0	1	0	0	1	0	0	1	1
A	42	1	1	1	1	1	1	0	0	0	1	0	1	1	0	0	0	0	0	1	1	0	1	1	1
	43	1	1	1	1	1	1	1	0	0	1	0	1	1	0	1	0	0	0	1	1	0	1	0	1
	44	1	0	1	0	1	1	0	0	1	1	0	0	1	0	1	0	0	0	1	1	0	0	1	1
	45	1	1	1	1	1	1	0	0	0	1	0	0	1	0	0	0	0	0	1	1	1	0	1	1
	46	1	1	1	0	0	1	0	0	0	1	0	0	1	0	0	0	0	0	1	1	1	0	1	1
	12	1	1	1	1	1	0	1	1	0	1	0	1	0	1	0	0	0	0	1	0	1	1	0	1
	13	1	1	1	1	0	0	1	0	0	0	0	1	0	1	0	0	0	0	0	0	0	1	1	1
	18	1	0	1	1	1	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	1	0
	21	1	1	1	1	0	0	1	1	1	0	1	0	0	1	0	0	0	0	0	0	0	0	1	1
B	22	1	1	1	1	0	0	1	1	1	0	1	0	0	1	0	0	0	0	0	0	0	0	1	1
	23	1	1	1	1	1	0	1	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	1	1
	25	1	1	1	1	1	0	1	0	1	0	0	1	0	0	0	0	0	0	0	1	0	1	1	0
	26	1	1	1	1	1	0	1	0	1	0	0	1	0	1	0	0	0	0	1	1	0	0	1	0
	28	1	1	1	1	1	0	1	0	1	1	0	0	0	0	0	0	0	0	0	1	0	1	0	
	32	1	0	1	0	1	0	1	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0
	8	1	1	1	1	1	0	0	0	1	0	0	1	0	0	1	1	1	0	1	0	1	0	1	1
	16	1	1	1	1	1	0	0	1	1	0	0	0	0	0	0	0	0	1	0	1	0	1	1	
	17	1	1	1	1	1	0	0	0	0	0	0	0	0	1	1	1	0	0	1	0	1	0	1	1
T	19	1	0	1	1	1	0	0	0	0	1	0	0	1	1	0	0	0	0	0	0	0	1	0	0
E	20	1	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
T	24	1	1	1	1	1	0	0	0	0	1	0	0	0	1	0	1	0	0	1	1	0	0	1	1
R	C 27	1	1	1	1	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0
A	29	1	1	1	1	1	0	0	0	1	1	0	0	0	1	0	0	0	0	0	0	0	0	1	0
D	30	1	0	1	1	1	0	0	1	1	1	0	0	0	0	0	0	0	0	0	1	0	0	1	1
S	31	1	1	1	1	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	1	0
	34	1	0	1	1	1	0	0	0	1	0	0	1	0	0	0	0	0	0	0	1	0	1	1	0
	39	1	1	1	1	0	0	0	0	0	1	0	0	1	1	1	1	1	1	0	1	0	0	1	0
	40	1	1	1	1	1	0	0	1	0	1	0	1	0	0	0	0	1	0	0	0	0	1	1	0
	41	1	1	1	1	1	0	0	0	0	1	0	1	1	0	0	0	0	0	0	1	0	1	1	1
	1	1	1	0	1	0	0	0	0	0	1	0	0	0	1	1	1	0	0	1	0	1	0	1	0
	4	1	1	0	1	0	0	0	0	0	1	0	0	1	0	1	1	0	0	1	0	1	0	1	1
D	5	1	1	0	1	0	0	0	0	0	1	0	0	1	0	0	0	0	0	1	0	1	0	1	1
	11	1	1	0	1	0	0	0	0	0	1	1	0	1	1	0	1	0	0	1	0	1	0	1	1
	10	1	1	0	1	1	0	0	0	0	1	1	0	0	1	1	1	0	0	1	0	1	0	0	1
	2	1	1	0	1	1	0	0	0	0	0	0	0	0	1	1	1	0	0	1	0	1	0	1	0
	3	1	1	0	1	1	0	0	0	0	0	0	0	0	1	1	1	0	0	1	0	1	0	1	0
	6	1	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	1	1
E	7	1	1	0	1	1	0	0	0	1	0	0	0	0	1	0	0	0	0	1	0	1	0	1	1
	14	1	1	0	1	1	0	1	1	1	0	0	1	0	1	0	0	0	0	0	0	1	0	0	1
	15	1	1	0	1	1	0	1	1	1	0	0	0	0	1	0	0	0	0	1	0	1	0	0	1
	9	1	1	0	1	1	0	0	0	0	0	0	1	0	1	1	1	1	0	1	0	1	0	1	1
	33	1	1	0	1	1	0	1	0	1	0	0	1	0	0	0	0	0	0	0	1	0	1	1	0
F	48	1	0	0	0	0	0	1	0	0	1	0	1	0	0	0	0	0	0	0	1	0	1	1	0
	49	1	0	0	0	0	0	1	0	0	1	0	1	0	0	1	1	0	0	0	1	0	1	1	0
	47	1	0	0	0	0	1	0	0	1	1	0	0	1	0	1	1	0	0	1	1	0	0	1	1

Table 6.1 shows the habitat matrix so constructed. The table shows the presence (indicated by a '1') or absence (indicated by a '0') of a habitat component (as listed above) in a named tetrad (as shown in Figure 6.1). This matrix was then used to classify the habitat as follows. 'Key' habitat components were selected which either divided the tetrads into roughly equal sub-sets, or were considered to reflect the major habitat divisions represented by the habitat description given in chapter 2. The first division was made on the presence or absence of Sycamore as a standard tree. Within that group which contained Sycamore, a further subdivision was made on the presence or absence of Beech as a standard tree since its importance to Great tits was well established. Tetrads containing Sycamore but not Beech were subdivided further on the presence of even-aged coniferous plantation. Tetrads lacking Sycamore contained both the ancient semi-natural woodland habitats which contained Maple, and the post-war plantations of Radbrooke Common which did not. The ancient semi-natural woodland (Great wood) tetrads were further divided on the presence or absence of pioneer scrub since those with scrub have been rather more disturbed (especially by burning) than other parts.

This 'divisive monothetic' classification (see Poole 1974) produced six habitat types which adequately reflect the broad habitat description given earlier. Figure 6.2 shows the derivation of this classification. Since the 'key' components were chosen subjectively, a test was carried out to check that the divisions reflected statistically significant associations of habitat components. The similarity between a tetrad and any other is given by:

$$\frac{\text{The number of shared components}}{\text{The total possible } (=24)}$$



habitat	A	B	C	D	E	F
tetrads	9	10	14	5	7	4
nest-boxes	42	47	84	44	60	16

Figure 6.2. Dendrogram showing the derivation of the habitat classification used in the present analyses. Tetrads were divided on the presence (+) or absence (-) of the 'key' habitat component shown. The number of tetrads in each of the six habitat types so derived is given at the bottom of the diagram.

For example tetrads 35 and 36 share 21 of 24 components. The similarity between them is 21/24 = 0.875. The mean similarity among tetrads within a habitat type was calculated by comparing each tetrad with every other within its habitat type. The similarity between each tetrad and every other in different habitats was then calculated. Table 6.2 shows the mean habitat similarity among tetrads within and between habitat types.

Tetrads were significantly more similar within habitat types than between them (t_{2141}=13.59, P<0.0001). Hence, although derived subjectively, the divisions made using the 'key' habitat components represented 'real' differences in habitat. Classified in this way, no tetrad changed its habitat class (due to coppicing etc.) during the study. Figure 6.3 shows the distribution of habitat types through the study area and Figure 6.4 shows the relationship between this distribution and altitude. Table 6.3 summarises the characteristics of each habitat type and shows the distribution of birds sampled in each. This classification was used in an ANOVA to analyse variation in bill characters.

6.2.1b The distribution of Great tits by habitat.

Over the four breeding seasons (1982-'85), the percentage occupancy of boxes differed significantly among habitats from that expected from the relative availability of boxes (X^2_5=12.39, P<0.05, Goodness-of-fit-test). Habitats A to C were used rather more than expected whilst habitats D to F were used rather less. This probably reflects the very high density of boxes in habitats D and E (Great Wood - see Minot & Perrins 1986) rather than the differential settlement of birds by habitats since it does not agree with the fidelity rates of breeding adults to a habitat shown in Table 6.4. Further,

Table 6.2 The mean similarity of tetrads within and between habitat types.

Habitat	Mean similarity ± 1sd of tetrads within habitat types.	n.	Mean similarity ± 1sd of tetrads between habitat types.	n.
A	Ø.762 ± Ø.Ø9Ø	36	Ø.586 ± Ø.Ø96	36Ø.
B	Ø.7Ø6 ± Ø.113	45	Ø.657 ± Ø.112	39Ø.
C	Ø.7Ø5 ± Ø.1Ø4	91	Ø.642 ± Ø.1Ø8	49Ø.
D	Ø.833 ± Ø.Ø59	1Ø	Ø.614 ± Ø.1Ø9	22Ø.
E	Ø.794 ± Ø.1Ø3	21	Ø.619 ± Ø.117	294.
F	Ø.688 + Ø.16Ø	6	Ø.563 + Ø.117	18Ø.
Overall mean	Ø.7297 ± Ø.1Ø97	2Ø9	Ø.62Ø8 ± Ø.1132	1934.

t_{2141}=13.59, P<Ø.ØØØ1.

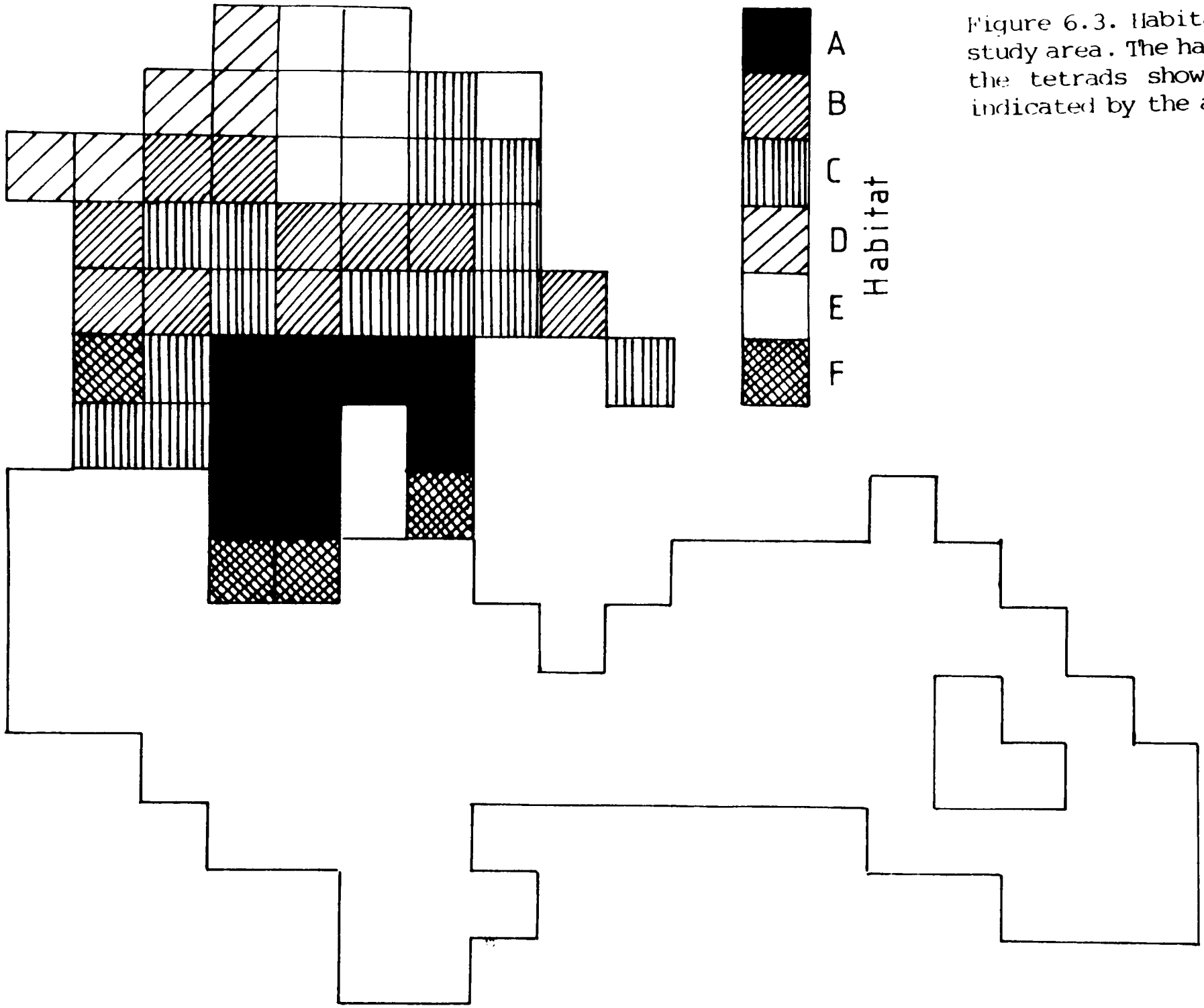


Figure 6.3. Habitat map of the Wytham study area. The habitat type in each of the tetrads shown in Figure 6.1 is indicated by the appropriate shading.

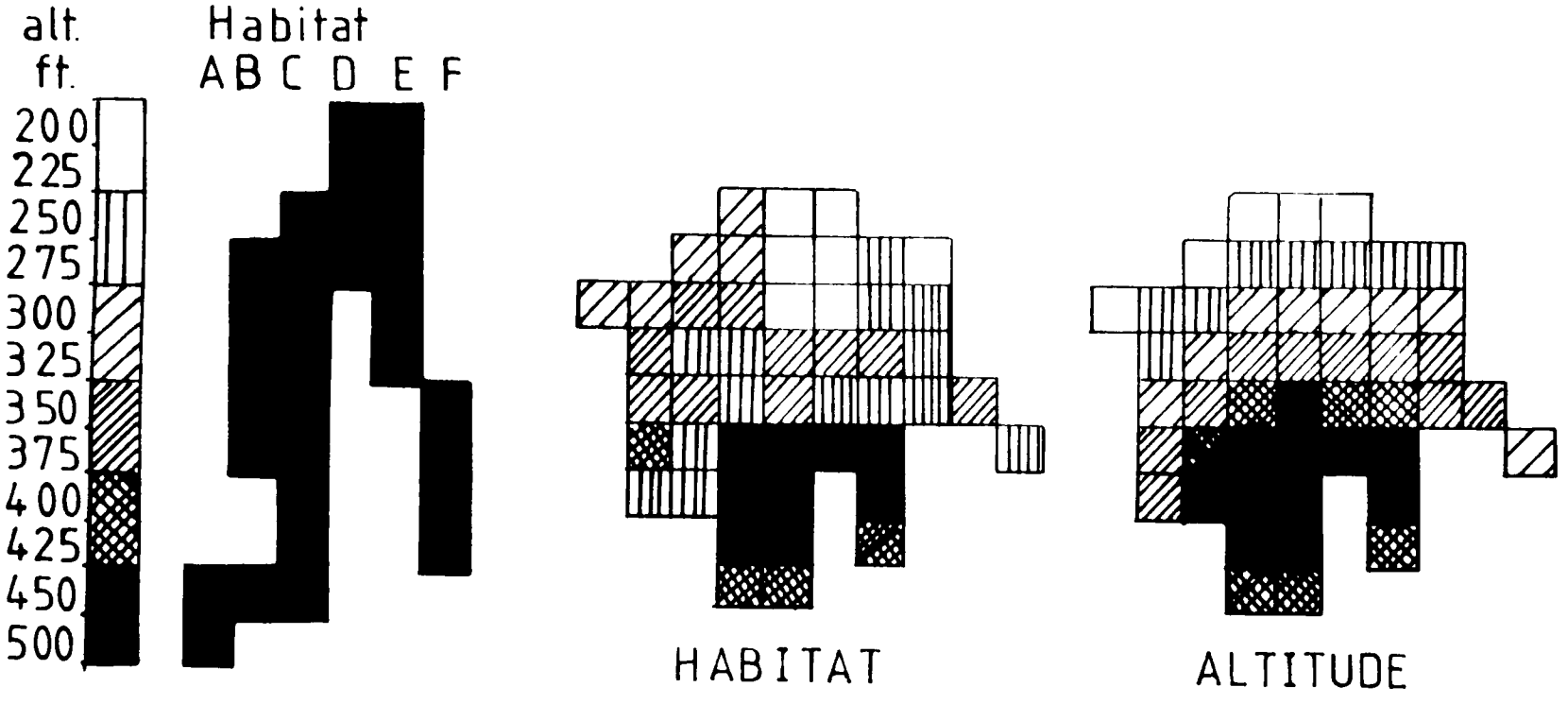


Figure 6.4. Map showing the distribution of habitat types (as Figure 6.3) in the Wytham study area in relation to altitude as shown in the left-hand diagram. The key to habitat shading is as given in Figure 6.3. The key to altitude (mean height O.D. for the tetrad) is given on the left.

Table 6.3 The principal features of Wytham habitats.

Habitat	Altitude	Habitat description	No. nest boxes	No. Adults sampled male	female	total
A	high	Mature Beech wood - winter trapping area.	42	59	61	120
B	medium	Mature Sycamore wood & conifer plantation.	47	62	63	125
C	medium	Mature Sycamore wood without conifers.	84	103	94	197
D	low	Disturbed ancient semi-natural woodland.	44	33	34	67
E	low	Ancient semi-natural woodland.	60	55	61	116
F	medium-high	Mostly broad-leaved plantation < 50yrs.	16	15	14	29
		Totals:	293	327	327	654

the distribution of birds by age did not differ significantly from a random expectation (X^2_5=9.224 for males, n.s, 3.499 for females, n.s). Nor did the numbers of immigrant and resident breeders differ significantly from a random expectation (analysed within age/sex classes) as is shown in Appendix 2. Hence there was no evidence for a net age-related movement of birds between habitats as has been suggested for habitats differing rather more in quality than the present ones (Krebs 1971, Ulfstrand et al. 1981).

Despite the lack of differences in age ratio or immigrant/resident ratio among habitats, there were nevertheless significant differences in habitat quality reflected in the mean fledging date and weight of chicks. And this in turn was reflected in the fidelity of breeding individuals to a habitat (the percentage of breeders that were known to be alive that bred in the same habitat in two years). This is shown in Table 6.4. Figure 6.5 shows the relationship between the mean chick weight (averaged over four years) for a habitat type and the percentage fidelity of breeding adults to a habitat type. Although not significant, this relationship accounted for 43.5% of the variation in a linear model.

Neither fledging date nor the fledging weight correlated significantly with altitude, nor were fledging date and weight themselves correlated across habitats (r_4=-0.102). Since habitats did not differ significantly in age ratios etc, it is believed that these differences in fledging date and weight reflect real differences in habitat quality.

Table 6.4. Variation in chick 15th day date, weight, and parent fidelity among habitat types. Dates and weights were standardised for year differences.

Habitat	N	Mean weight Deviation.	Mean ± 1sd Weight.	Mean ± 1sd 15th Date. (May 1=1)	% Fidelity.
A	54	-Ø.ØØ2	18.67 ± Ø.1Ø	36.42 ± Ø.99	85.2
B	54	-Ø.Ø29	18.65 ± Ø.12	35.7Ø ± 1.Ø2	66.7
C	91	+Ø.ØØ1	18.68 ± Ø.1Ø	36.Ø1 ± 1.Ø3	72.Ø
D	27	+Ø.Ø48	18.72 ± Ø.Ø9	36.13 ± Ø.63	76.9
E	46	+Ø.Ø17	18.69 ± Ø.Ø8	36.15 ± Ø.9Ø	86.7
F	14	-Ø.Ø35	18.64 ± Ø.Ø8	36.6Ø ± 1.22	42.9
			$F_{5,28Ø}=2.82$ P<Ø.Ø5	$F_{5,28Ø}=3.87$ P<Ø.Ø1	

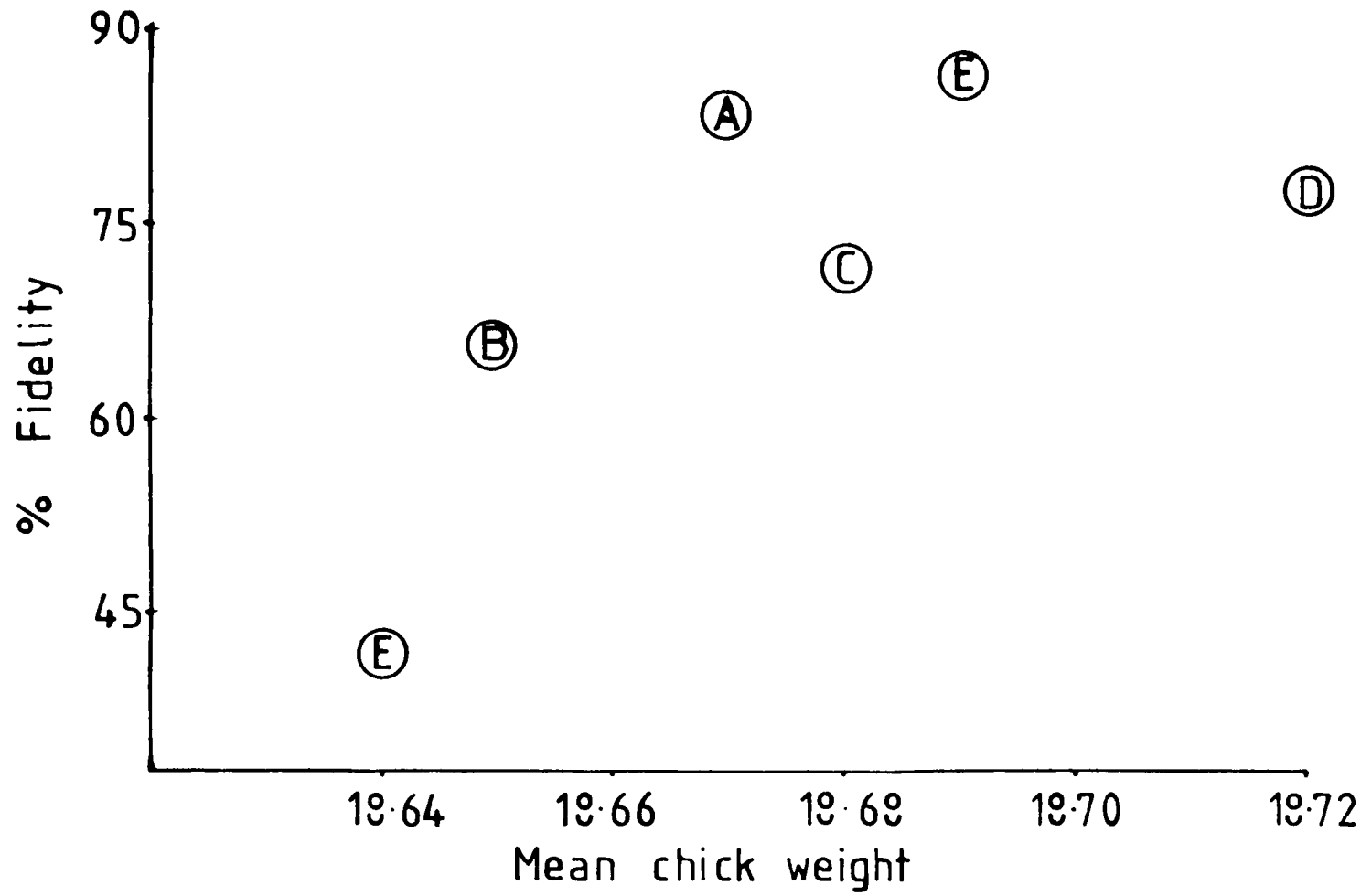


Figure 6.5. The relationship between parental fidelity (to a habitat type) given by the % of breeders that were known to be alive, that stayed in the same habitat type, and mean chick weight at 15 days across habitat types.

6.2.2 Indirect methods of assessment.

To examine the influence of habitat on bill size within individuals, data were used from all measured individuals that bred in more than one year. Over four years, this gave a sample of 160 paired observations (75 male, 85 female - note also that these are observations of 160 different individuals). Initially, these data were analysed in relation to the habitat classification described above. Hence, within each sex, the mean change in bill length between years of birds that changed the habitat type in which they bred (between those years) was compared (by t test) with the mean change in bill length of those birds that stayed in the same habitat type (the control group). However no significant difference was found in the bill length changes of birds that changed habitats and the control group. This may indicate more about the habitat classification than the variation in bill size. Hence an alternative method was used which looked only at changes in location rather than habitat specifically. This is a more general approach than the habitat analyses already carried out and is described below.

Each pair of observations was given a score depending on whether the bird had stayed in the same nestbox, tetrad or woodland compartment (as described in chapter 2). This geographical index allowed comparisons of measurements to be made along a scale of individual movement. It was calculated as follows. With respect to the nestbox, tetrad or compartment, each bird was scored as 0 or 1 depending on whether the location was the same or different in the two years. The nestbox, tetrad and compartment levels were themselves labelled as 1, 2 and 3 respectively. Within each pair of observations, the location score (0/1) was multiplied by the location level (1-3) and these products were then summed to give the final index. The method is clarified by an example:

To calculate the geographical index of movement between breeding sites between years. The example is for a bird changing nestbox and tetrad but staying in the same compartment:

	location	nest		tetrad		compartment	
movement level	(a)	1		2		3	
location score	(b)	1		1		0	
product of a x b		1	+	2	+	0	sum = geographical index = 3.

For brevity the index was termed the Geogscore. Not all scores are possible by this method (within the range 0 - 6) since a bird staying in the same box must remain in the same tetrad and compartment. Table 6.5 gives the sample sizes available at each index level. This method gives an alternative (though less precise) measure of habitat difference. Note also that the probability that a change of territory has occurred increases with the Geogscore. This is not necessarily true for birds changing habitat. However, scores 0-3 are probably in the same habitat, whilst scores 4-6 are probably not.

Chi-square tests were carried out to determine whether the distribution of Geogscores differed significantly between years. None was significant. Since there was no 'year effect' in the tendency to change territories etc. the measurements of birds that stayed in the same nestbox or habitat provide a control for comparison with those that changed location. The degree of change in bill size (all characters) between years was compared among Geogscore levels by single-classification ANOVA. All analyses were carried for each sex separately.

Table 6.5. Further interpretation of the Geogscore and sample sizes available. See text for full details. Definition is given as nestbox (1), tetrad (2) and compartment (3). This was scored as Ø if the same in both years, or 1 if different in the two years.

Geogscore	Definition			Probable relationship	N males	N females	total
	1	2	3	to territory.			
Ø	Ø	Ø	Ø	same territory	25	28	53
1	1	Ø	Ø	same territory	24	17	41
3	1	1	Ø	may be same territory	13	19	32
4	1	Ø	1	may be same territory	4	3	7
6	1	1	1	Different territory	9	18	27
					75	85	

6.3 Results.

6.3.1 Results of the direct analyses.

Table 6.6 Shows the variation in bill length across habitats. Data from all years were pooled, but were standardised to remove between-year differences (which were themselves significant). No significant differences were found among habitats. However, in both sexes there was a tendency for individuals in the ancient semi-natural woodland habitats (D and E) to have longer bills. Table 6.7 shows that this difference was significant in females.

Males did not differ significantly in this way (t_{324}=1.57). However, whereas females did not vary in bill depth across habitats, males in ancient semi-natural woodland had significantly deeper bills than those in other habitats (Table 6.8). In males, wing and tarsus length also varied significantly across habitats (for wing: $F_{5,321}$=2.55, P<0.05; for tarsus: $F_{5,320}$=3.29, P<0.01). In tarsus length this was again largely because males in ancient semi-natural woodland were larger than those elsewhere (t_{324}=2.59, P=0.01). However, tarsus length was never correlated with either bill length or depth, either when analysed within or between habitats. Hence these are independent effects.

Table 6.6 Variation in bill length across habitats. Data were standardised between years.

Habitat	Mean ± 1sd of male bill length (Ø.1mm)	n	Mean ± 1sd of female bill length (Ø.1mm)	n
A	133.Ø6 ± 3.77	59	135.86 ± 3.94	6Ø
B	133.37 ± 4.3Ø	61	136.Ø9 ± 4.59	61
C	133.6Ø ± 4.Ø4	1Ø3	135.48 ± 5.13	111
D	134.23 ± 4.63	33	137.82 ± 5.38	33
E	134.18 ± 3.98	55	136.42 ± 4.33	61
F	133.25 ± 3.27	15	135.77 ± 3.76	14
	$F_{5,32Ø}$=Ø.65, NS		$F_{5,334}$=1.39, NS	

Table 6.7 Comparison of female bill length in ancient semi-natural woodland with other habitats.

Habitat	Mean ± 1sd of bill length (Ø.1mm)	n
Ancient semi-natural wood	136.91 ± 4.74	94
Other habitats	135.74 + 4.64	246

t_{338}=2.Ø47, P<Ø.Ø5

Table 6.8 Comparison of bill depth of breeding males (standardised between years) in ancient semi-natural woodland and other habitats.

Habitat	Mean ± 1sd of bill depth (Ø.1mm)	n
Ancient semi-natural wood.	46.93 ± 1.49	88
Other habitats	46.52 ± 1.54	238

$t_{324}=2.14$, $P<Ø.Ø5$

6.3.2 Results of the indirect analyses.

I stated above that there was no difference between the mean absolute change in bill length of birds that stayed in the same habitat type and those that changed habitats between years. To attempt to relate bill length changes more specifically to changes in habitat, I carried out single-classification ANOVAs on bill length changes (between years) across different changes in habitat. In both sexes, habitats differed significantly in their contribution to the overall pattern. The result was the same when the bill lengths were first transformed logarithmically to equalise the variances between habitat-change categories. However, since the sample sizes were frequently small (sometimes n=1), no clear pattern emerged to show which habitats were particularly responsible for changes in bill length. Table 6.9 shows the overall variation in bill length changes among specific habitat changes.

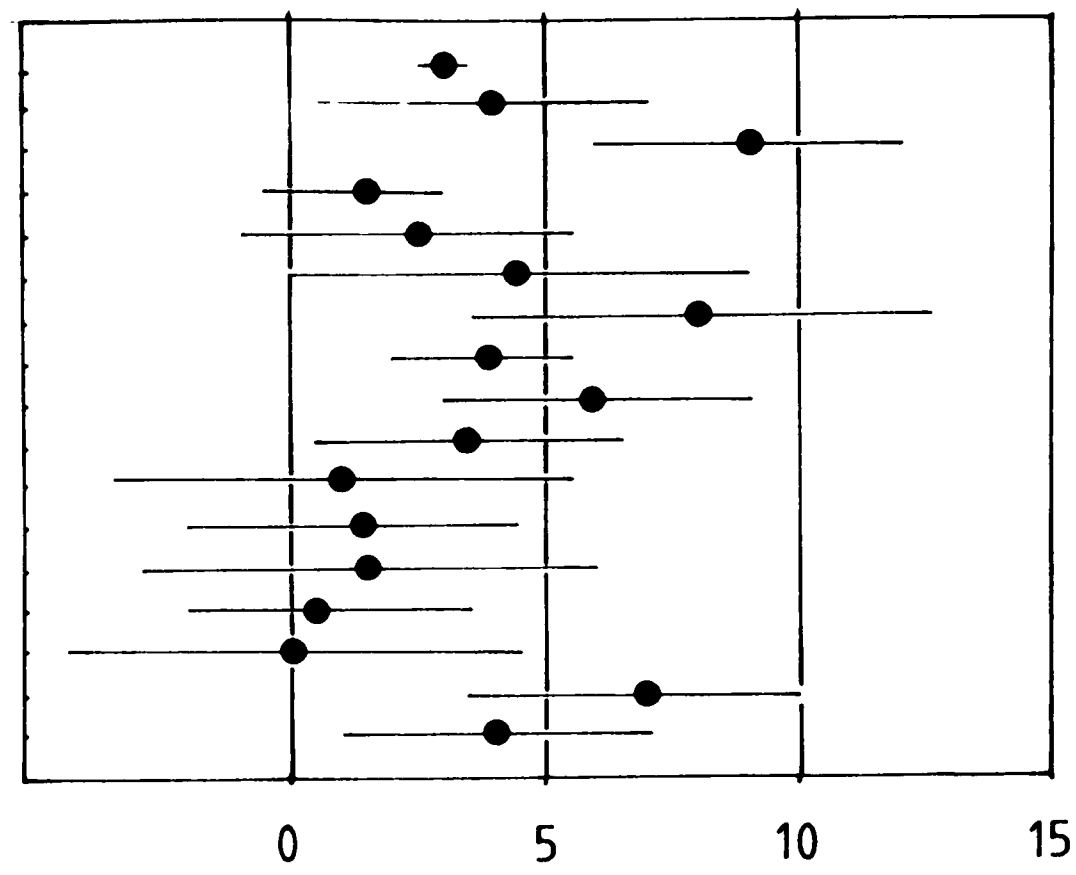
Although within habitats, the bill lengths of paired individuals (ie: across breeding pairs) were not correlated, Figure 6.6 shows that across habitats they were highly correlated (r_{22}=0.594, P<0.01). Data were first standardised within sexes to remove year effects. This indicates that habitats with long- or short-billed males also had long- or short-billed females respectively. This gives some of the strongest evidence for a habitat effect on bill length.

Table 6.10 shows the absolute change in bill length of breeding adult Great tits grouped by Geogscore. Sexes are shown separately. Although in males a change in location was not associated with a change in bill length (as was seen in the analysis with habitat type), those females that changed breeding site

Table 6.9. The mean absolute change in bill length of Great tits (sexes combined) that changed their breeding habitat between years. The left-hand column shows the specific change in habitat, eg: the entry A-C are those individuals that moved from habitat A to habitat C etc. The sex-specific ANOVA results are given below. Note that after log. transformation of the data, the F ratio for the sexes combined was $F_{16,143}$=2.01, P<0.01.

Habitat change	Mean ± lsd	n
no change	3.00 ± 2.00	120
A-C	3.75 ± 0.35	2
A-F	9.00 ± 5.66	2
B-C	1.31 ± 0.46	8
B-D	2.25 ± 0.35	2
B-F	4.50 ± 0.00	1
C-A	8.00 ± 0.00	1
C-B	3.75 ± 2.55	8
C-D	6.00 ± 7.07	2
C-E	3.50 ± 4.24	2
C-F	1.00 ± 0.00	1
D-B	1.25 ± 1.77	2
D-F	1.50 ± 0.00	1
E-C	0.67 ± 0.29	3
E-D	2.79 ± 1.96	1
F-B	6.75 ± 3.18	2
F-C	4.00 ± 1.41	2

Males $F_{11,63}$= 1.97, P<0.05
Females $F_{13,71}$= 2.66, P<0.01
Combined $F_{16,143}$=2.53, P<0.001



Mean ± 95% confidence interval of change in bill length (×0·1mm).

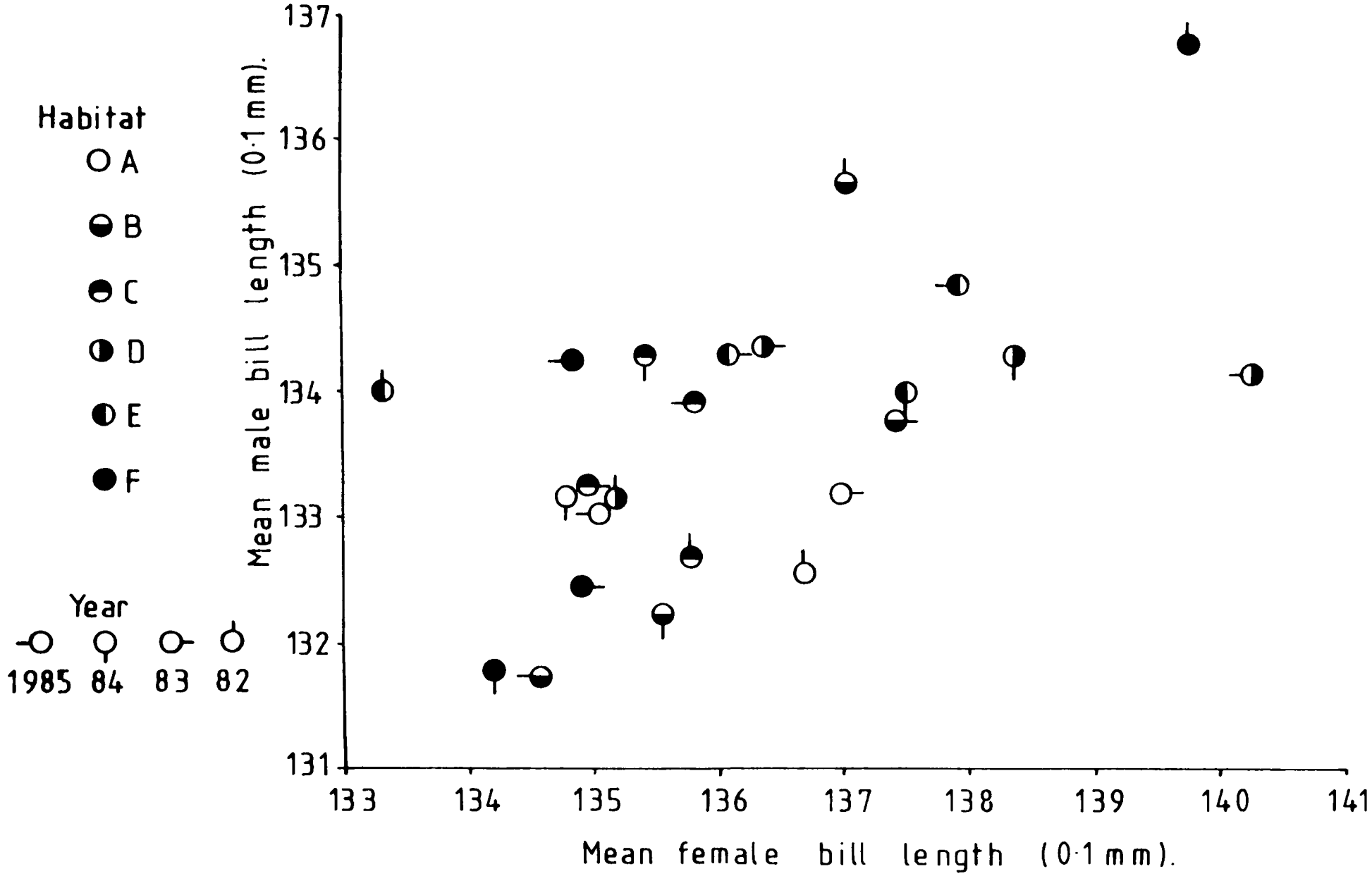


Figure 6.6. The relationship between mean male and female bill lengths in each habitat type in each year. Data were first standardised to remove between-year differences in the means.

showed a significantly greater change in bill length than females that stayed in the same location. Table 6.11 shows the ANOVA table for females analysed across Geogscores. 11.8% of the variation in bill length between years in females was 'explained' by the change in breeding site. Table 6.10 shows that females changing woodland compartment (scores 4 and 6) contributed most to this result. When these birds were compared with those that stayed in the same compartment (scores 0 to 3), the difference was more striking as shown in Table 6.12.

Further, in the year preceeding a change of compartment, females that changed compartments between years differed significantly in bill length from those that stayed in the same compartment. However, in the year following a change of compartment, there was no significant difference in bill lengths of the two groups. These results are shown in Table 6.13. This was accompanied by a significant reduction in overall variance between years ($F_{84,84}=1.65$ $P<0.05$). These two facts together suggest that longer-billed females were more likely to change compartments than short-billed females. The cause of this relationship is not clear.

Similar tests were carried out on bill depth, bill index and body weight (corrected for time of day) within sexes. None differed significantly between groups. Since these results were not confounded by year effects, it is likely that the breeding location has an observable effect on bill length. Further that this effect is observable at the level of the compartment. Since this scale most probably corresponds to a change in habitat, this is probably a habitat effect. However, it is interesting that males were not so affected and I shall consider this briefly in the next section.

Table 6.1Ø Changes in bill length between years in male and female breeding Great tits by Geogscore. See text for details.

Geogscore	Mean ± 1sd of male bill change (Ø.1mm)	n	Mean ± 1sd of female bill change (Ø.1mm)	n
Ø	2.82 ± 2.42	25	2.63 ± 2.Ø3	28
1	3.15 ± 2.Ø1	24	2.35 ± 2.3Ø	17
3	3.5Ø ± 2.4Ø	13	2.53 ± 1.72	19
4	3.25 ± 2.5Ø	4	6.33 ± 4.Ø4	3
6	3.ØØ ± 3.42	9	3.97 ± 3.52	18
	$F_{4,7Ø}$=Ø.18,NS.		$F_{4,8Ø}$=2.67, P<Ø.Ø5	

Table 6.11 Single-classification ANOVA carried out on the absolute change in female bill length between years across Geogscores.

Source of variation	D.F	S.S	M.S	F
Geogscore	4	65.56	16.39	2.67 P<Ø.Ø5
Error	8Ø	491.33	6.14	
Total	84	556.89		

Table 6.12 Changes in bill length between summers in female Great tits remaining in the same compartment compared with those that changed compartment.

Location	Mean ± 1sd of change in bill length (Ø.1mm)	n	
Same compartment	2.52 ± 1.99	64	$F_{1,83}$=8.27, P<Ø.Ø1
Different compartment	4.31 ± 3.59	21	

Table 6.13 Comparison of female bill length before and after changing compartment with birds which stayed in the same compartment (control)

Location	Mean ± 1sd bill length in first year	n	Mean ± 1sd bill length in second year	n
Same compartment	135.4 ± 4.5	64	135.Ø ± 3.7	64
Diff. compartment	138.4 ± 5.9	21	135.1 ± 4.7	21
	t_{83}=2.14, P<Ø.Ø5		NS	

6.4 Discussion.

Whilst there is apparently evidence that bill length varied among habitats during the breeding season, the pattern of variation was not well defined. Indeed some results may even appear to conflict. For example, females which changed compartments between years, changed their bill length more than a those that stayed in the same compartment, though this was not seen in relation to a change in habitat type. This suggests that compartments differed more than defined habitat types in those environmental components that influenced bill length. Further, females seemed to be more influenced than males.

Throughout this chapter I have implied that any association between bill length and habitat resulted from an influence of the habitat on bill length. However, I have not demonstrated that birds did not select their breeding habitat partly on the basis of their bill lengths. This should be borne in mind during the following discussion although I shall not consider it further.

The apparent sex-difference in response to habitat types raises the possibility that the differences in the change in bill length reflected differences in winter activity rather than the change in habitat itself. That is, females which changed habitats differed ecologically in winter from those that remained in the same habitat. To test this, I examined the winter capture frequencies of females in the two groups (same/different compartment). Table 6.14 shows that females that changed compartment between summers were equally likely to be trapped in Wytham during the intervening winter than those that remained. Whilst this does not prove that the birds were not segregated in winter, it suggests that they were not. Hence the difference in the change of bill length between groups was probably due to a habitat effect.

Table 6.14 Comparison of winter trapping frequencies for females retaining or changing breeding habitat between years.

	winter trapped	Not winter trapped	totals
Same compartment	12	52	64
Diff. compartment	2	19	21
Totals	14	71	85

X^2_1=Ø.98, NS.

It is not clear why the change in bill length with habitat was observed only in females. I have suggested that individuals may execise some active control of bill size by bill wiping and moult and that this was observed mostly in males. Table 6.15 shows the percentage of males undergoing bill moult in each habitat together with expected frequencies in 1984. Taken across all habitats the percentage of males in bill moult did not differ significantly from the random expectation. However, in habitats C and D, significantly more individuals showed bill moult than was expected. Although not strong evidence, it is possible that active bill-size regulation by moult could obscure the effect of habitat in males. Tables 6.8 and 6.9, and Figure 6.6 suggested that bill size was not independent of habitat in males. These results indicate again the importance of immediate environment in determining bill size.

Although a functional explanation for habitat effects cannot be demonstrated at this stage, one further observation might be mentioned. I have shown that when present, the relationship between bill length and prey size was negative. Breeding adults in the Great Wood (habitats D and E) had significantly longer bills than those in other areas. Table 6.16 shows that mean prey size (estimated from chick faecal analysis) was significantly smaller in the Great Wood (data from 1984 when bill length and prey size were correlated) than in the other rounds. However no causal relationship should be inferred from this at present.

Table 6.15. The distribution of bill moult in breeding male Great tits in 1984 by habitats.

Habitat	N birds	N in moult	Observed %	Expected N.	
A	14	4	28.57	5.29	
B	13	2	15.38	4.92	
C	21	11	52.38	7.94	$X^2_1=6.46$
D	13	10	76.92	4.91	$P<0.05$.
E	16	4	25.00	6.05	
F	5	0	0.00	1.89	
	82	31	Overall $X^2_5=11.09$, NS.		

Table 6.16. Comparison of mean prey size (caterpillar mandible length xØ.1mm) between nestbox rounds. Data are for 1984.

Nestbox round	N nests	Mean ± 1sd caterpillar mandibles (Ø.1mm)	n	
Great Wood	12	Ø.64 ± Ø.25	95	
Extra	19	Ø.85 ± Ø.25	153	Mean of Extra
and				
Common Piece	4	Ø.94 ± Ø.16	13	Common Piece =
			261	Ø.86 ± Ø.24,

n=166.

t_{259}=6.799, P<Ø.ØØ1

Chapter 7. Natural selection of and for bill characters.

Chapter 7. Natural selection of and for bill characters.

7.1 Introduction.

Evolutionary adaptation (sensu Bock & Wahrlert (1965) - see chapter 4) results from the differential survival of phenotypes, resulting from differences in fitness (sensu Endler 1986). Through inheritance, this leads to the differential survival of genotypes and hence changes in gene frequencies within populations - natural selection (Darwin 1859, Huxley 1940, Huxley 1942) combined with gene flow. Endler (1986) considers that natural selection is the predictable result of variation, fitness differences and inheritance within populations that are not at equilibrium. However, despite this apparently deterministic quality, natural selection poses many practical problems both in its recognition and measurement. Whereas the demonstration of variation, fitness differences and even heritability are relatively accessible to study in natural populations, the demonstration of natural selection itself is far less so. Endler (1986) reviews the problems associated with its detection, and I shall briefly discuss those relevant to the present study in the next section of this chapter.

An important consideration in the study of bill character selection, is the relative variance contribution that is genetic. In Geospiza, the heritability of bill characters was high (Boag & Grant 1978, Boag 1983). Consequently, bill characters responded rapidly during a period of intense selection for bill size (Boag & Grant 1981). This is probably the best documented case of natural selection for bill size in a marked, wild population.

Similarly, Smith & Dhondt (1980) demonstrated high genetic determinism in the bill size of the Song sparrow Melospiza melodia. By brood manipulation, they showed that offspring bill size correlated significantly with that of the true parents, but not with the foster parents. Of three bill characters examined, h^2 was highest for bill depth at 50.6% (Smith & Zach 1979). However, in a similar experiment with Red-winged Blackbirds Agelaius phoeniceus, James (1983) found that fledgling bill size correlated significantly better with that of the foster parents than with the true (genetic) parents. It remains to be seen whether these results reflect general differences in bill character heritability between seed and insect-eating species.

Related to problems associated with heritability, are those arising from phenotypic plasticity, and particularly - seasonal variation. 'Adaptive plasticity' not only buffers individuals against selection, but it also presents methodological problems which will be considered in the next section.

The speed with which gene/morph frequencies will change under selection is partly a function of the heritability of the character considered. Correlations among characters under differential or opposing selection may lead to either a reduced rate of morphological change, no observable change, or change in a character not directly under selection, but correlated with a selected character. This is selection of a character through selection for an associated character (Sober 1984, Endler 1986). Grant (1985) has identified selection of correlated bill characters in Geospiza conirostris.

Endler (1986) describes ten methods for detecting natural selection in natural populations. However, these differ markedly in the conclusiveness of their results. Endler's method vii (genetic demography or cohort analysis) - the longitudinal study (Falconer 1981), although time-consuming, gives the

best evidence for selection. This method follows marked individuals and seeks to relate differences in survival to measured differences in traits that are believed to be relevant. The present study was carried out in this way.

There have been few studies of natural selection on or for bill characters. The most important is that of Grant and his co-workers in Galapagos (see Boag & Grant 1978, Price et al. 1984 and Grant 1985). These studies show the intermittent nature of selection. That is, selection coefficients may change seasonally (Hespenheide 1973). They also showed that selection may act consistently in the same direction on successive selective occasions. Price et al. (1984) found that in each of three selective episodes, bill depth was most strongly selected, and always in the same direction. However, as Hespenheide (1973) points out, in a temperate, seasonal environment, there is no a priori expectation that directional selection should be consistent between selective events since different environmental conditions may favour different morphological solutions. Nor indeed need selection act equally upon all age or sex classes within a season. For example, in the present study, niche segregation could expose the sexes to different selection pressures.

In this chapter I have attempted to demonstrate the occurrence of natural selection both of and for bill characters. Evidence for directional, stabilising and disruptive selection are described. However, although the intensity of selection is sometimes reflected in the results, I have been concerned primarily with the demonstration of selection itself rather than with its measurement, and have, therefore, not calculated selection coefficients.

7.2 Methods.

Of the ten methods which Endler (1986) lists for the detection of natural selection, two are particularly valuable and might seem applicable to the present study. Method viii - 'comparison among age-classes or life-history stages' assumes that differences among age classes (in a cross-sectional analysis) are due to selection. That is, it assumes that selection has acted consistently among cohorts. In the present study, I have shown that phenotypic plasticity is a major contributor to total variation so that this assumption may not be made. In particular, differences among age-classes were season-specific. Hence method viii is not applicable to this study. The second method, method vii (cohort analysis) has therefore been used here.

Cohort analysis is not free from problems. In 'hard' morphological characters (see glossary) it should be possible to sample the same cohort at intervals. Then, assuming that biases in capture rate are constant among samples, any significant change in the mean or variance with time is due to directional or stabilising selection. In a 'soft' morphological character (see glossary) such as body weight or bill length, this method is rarely valid because changes in the mean or variance may arise by seasonal or socio-ecological (eg: dominance mediated niche occupancy) variation. Hence only very strong selection might be detected in this way. That is, where the variation between samples was significantly greater than expected from seasonal (or other) variation alone (as determined from repeatability analysis). In this case selection is detected retrospectively (eg: Perrins 1963, 1965).

Cohort analysis may also suffer from sampling bias if related to the character considered. However, the method has potential for absolute

measures of selection. For example, breeding Great tits show strong site fidelity between summers. Brown (1969) and O'Connor (1980) suggested that sub-optimal habitat might act as a 'buffer-zone' for tit populations. However, Krebs (1971) showed that in Wytham, even in sub-optimal habitat, adult Great tits were reluctant to vacate their breeding territories if space became vacant in optimal habitat (first year birds were more likely to change habitats within seasons). For this reason, birds found breeding in successive years are assumed to represent most of the survivors from the previous year. Further, it is generally assumed that survivorship estimates made in this way are very accurate (Perrins 1979, Clobert et al. in prep.). In this case a significant difference in the mean or variance of morphological characters between survivors and non-survivors as measured in the initial (base) population must be due to selection. However, it can only reflect selection acting on the variation as it was when measured. This may differ from that when selection actually occurred.

In the following analyses, 'survivors' are birds known to be alive after some specified period. 'Non-survivors' are all others. Hence non-survivors include survivors that were not trapped. In summer these categories may be interpreted more or less literally (for the reasons described above). In winter there may be bias caused by an association between niche occupancy and morphology. Any bias present is reduced in a retrospective analysis because it accepts that the base population may be a biassed sub-sample and examines the evidence for selection from within that sub-sample.

Two series of analyses were carried out to identify natural selection of bill characters in full-grown individuals (section 7.3). All bill characters were analysed. Since body-weight is known to predict survivorship during the

first 3 months of life (Perrins 1963, 1965), this was also included. In the first series of analyses, evidence for directional selection was sought by comparing the means (by t test) of survivors and non-survivors. To avoid problems associated with phenotypic plasticity, all analyses were carried out retrospectively (that is, on data from the base population). Hence two seasons have been specified in each case: (1) The season in which measurements were taken (base population); (2) The period over which survival was measured. Comparisons were made within age and sex classes, between summers (12 month selection period) and between winter and summer (6 month selection period). Summer to winter analyses were not carried out because it is important that the winter sample was taken as the base population to avoid bias (as explained above).

Secondly, evidence for stabilising selection was sought by comparing the variance (by F ratio test) of survivors with that of the whole base population. Data were analysed in the same groupings as described above and the analyses were again carried out retrospectively. Table 7.1 gives sample sizes available for analyses carried out on full-grown individuals.

Finally, in section 7.4 a retrospective analysis of survival in relation to bill depth was carried out in the 433 nestlings described in chapter 3 (section 3.5).

Table 7.1 Sample sizes available for bill comparisons in each season. The table shows the number of survivors and the total population (hence non-survivors = the total - survivors). The summer season is defined as in chapter 2. The winter season contains both the autumn and spring seasons defined in chapter 2. Note also that summer to summer comparisons were not carried out within age-classes (see text below).

	Survivors				Total			
Season	Males		Females		Males		Females	
	1Y	Ad	1Y	Ad	1Y	Ad	1Y	Ad
Su'82-Su'83	-23-		-25-		-61-		-71-	
Wi'82/3-Su'83	41	2Ø	3Ø	15	1Ø1	44	85	25
Su'83-Su'84	-21-		-25-		-112-		-124-	
Wi'83/4-Su'84	3	16	1	14	66	1Ø1	34	74
Su'84-Su'85	-25-		-31-		-81-		-91-	
Wi'84/5-Su'85	7	1Ø	5	2	134	67	161	5Ø

7.3 Differential survival of adults in relation to bill characters.

Table 7.2 shows the significance levels of t test comparisons for each bill character and for body weight carried out between summers. Since all members of the base population were at least one year old (and breeding), and age was not a contributor to bill variation in summer (section 3.3), comparisons were made within sexes but with age-classes pooled.

Only females in the summer of 1984 showed differential survival with respect to a bill character. Females surviving to breed in 1985 had had significantly shorter bills than non survivors. Note also that body weight was not a determinant of survival. Body weights were not standardised for body size so that this also contains a body size component. However, this method is the same as that used by Perrins (1963) in his analysis of post-fledging survivorship in relation to weight. Table 7.3 shows the results of variance comparisons carried out on the same groups of birds. Again, only females surviving from summer 1984 showed strong evidence of stabilising selection, in this case on bill index. Hence bill size in summer is a poor predictor of the probability of survival in adults.

Since bill size may change markedly between seasons, I repeated these tests on all classes, but taking the winter samples as the base populations. Table 7.4 shows the results of t test comparisons between survivors and non-survivors. Ten (out of 36) tests were significant (at least at $P<0.05$). This was considerably more than should be expected by chance, so that natural selection is strongly implicated. Again, body weight was relatively unimportant as a determinant of survival. First-year males surviving from the 1982/83 winter were significantly heavier than non-survivors, and this

Table 7.2. Evidence for directional selection of summer bill characters. In each case the base population is the first summer specified and the selection period is 12 months. The table shows the level of significance for t test comparisons between the means for survivors and non-survivors.

Season	sex	bill length	bill depth	bill index	weight
Su'82-Su'83	male	ns	ns	ns	ns
	female	ns	ns	ns	ns
Su'83-Su'84	male	ns	ns	ns	ns
	female	ns	ns	ns	ns
Su'84-Su'85	male	ns	ns	ns	ns
	female	**	ns	*	ns

Table 7.3. Evidence for stabilising selection of summer bill characters. In each case the base population is the first summer specified and the selection period is 12 months. The table shows the level of significance for F test comparisons between variances for survivors and the whole base population.

Season	sex	bill length	bill depth	bill index
Su'82-Su'83	male	ns	ns	ns
	female	ns	ns	ns
Su'83-Su'84	male	*	ns	ns
	female	ns	ns	ns
Su'84-Su'85	male	ns	ns	ns
	female	ns	ns	***

Table 7.4. Evidence for directional selection of winter bill characters. In each case the base population is the first winter specified and the selection period is approximately 6 months. The table shows the level of significance for t test comparisons between means for survivors and non-survivors.

Season	sex	age	bill length	bill depth	bill index	weight
Wi82/3-Su83	male	ly	ns	*	*	*
		Ad	ns	ns	ns	ns
	female	ly	ns	**	ns	ns
		Ad	ns	ns	ns	ns
Wi83/4-Su84	male	ly	ns	ns	ns	ns
		Ad	ns	ns	ns	ns
	female	ly	***	**	***	***
		Ad	*	ns	ns	ns
Wi84/5-Su85	male	ly	**	ns	*	ns
		Ad	ns	ns	ns	ns
	female	ly	ns	ns	ns	ns
		Ad	*	ns	ns	ns

reflects the greater amount of fat carried by these birds (see Appendix 3). In addition, a single first-year female surviving the winter of 1983/84 (when the emigration rate in this class was known to be high) was significantly heavier than others of its class. Table 7.5 shows the results of the variance ratio tests carried out on these groups. Only adult females in the winter of 1983/84 showed evidence for stabilising selection on the winter values, and this was for bill length.

Three general points may be derived from these results. First, and most importantly, is that the evidence for selection (either directional or stabilising) during the study period was extremely weak. Secondly, selection occurred most frequently in winter and was directional rather than stabilising. Thirdly, selection affected first-year birds more than adults (8/10 significant comparisons occurred within first-year classes) and females slightly more than males (6/10 significant tests were female) though not significantly. Adult males were never affected. It might also be noted that when selection of bill depth occurred, it always favoured deeper bills, whilst selection of bill length usually (3/4) favoured a shorter bill. It should also be noted that the apparently strong case of selection of body weight and three bill characters in 1983/4 first-year females concerned a single surviving individual, and those characters were uncorrelated in that particular class and season.

Table 7.5. Evidence for stabilising selection of winter bill characters. In each case the base population is the first winter specified and the selection period is approximately 6 months. The table shows the level of significance for F test comparisons between variances of survivors and the whole base population.

Season	sex	age	bill length	bill depth	bill index
Wi82/3-Su83	male	ly	ns	ns	ns
		Ad	ns	ns	ns
	female	ly	ns	ns	ns
		Ad	ns	ns	ns
Wi83/4-Su84	male	ly	ns	ns	ns
		Ad	ns	ns	ns
	female	ly	ns	ns	ns
		Ad	**	ns	*
Wi84/5-Su85	male	ly	ns	ns	ns
		Ad	ns	ns	ns
	female	ly	ns	ns	ns
		Ad	ns	ns	ns

7.4 Differential survival of offspring in relation to bill characters.

In section 3.5.2, I showed that the distribution of bill depth in retrapped individuals (survivors of 433 nestlings measured) was skewed with respect to sex. I suggested that this might reflect differential survival with respect to bill depth in the first three to six months after fledging. In this section I explore further this possibility.

Of 433 nestlings measured in the nest on day 15, 66 were subsequently retrapped. The original distribution of bill depth was presented in figure 3.4. Figure 7.1 shows the percentage of individuals of a bill depth class that were retrapped during the winter of 1984/85. Significantly more large-billed individuals were retrapped than expected. If winter sampling was unbiased relative to the distribution of bill depth in the nest (bill depth in the nest was poorly correlated with that in winter), this demonstrates strong selection of bill depth. However, in the nest, body weight was the most significant predictor of bill depth (18.7%, see Table 3.19), and this is known to be an important determinant of fledgling survival (Perrins 1963, 1965). Table 7.6 ~~shows the percentage of chicks of the 1984 cohort of each body weight class~~ shows the percentage of chicks of each body weight class of the 1984 cohort which were retrapped more than three months after fledging (n=550).

The correlation between relative fitness (% retrapped) and body weight 0.863 (df=7) was highly significant ($P<0.01$), and the relationship was essentially linear.

To establish whether bill depth was the target for selection (which might be implied by figure 7.1), I regressed bill depth on body weight and repeated the analysis of relative fitness on the residual variation in bill depth. The

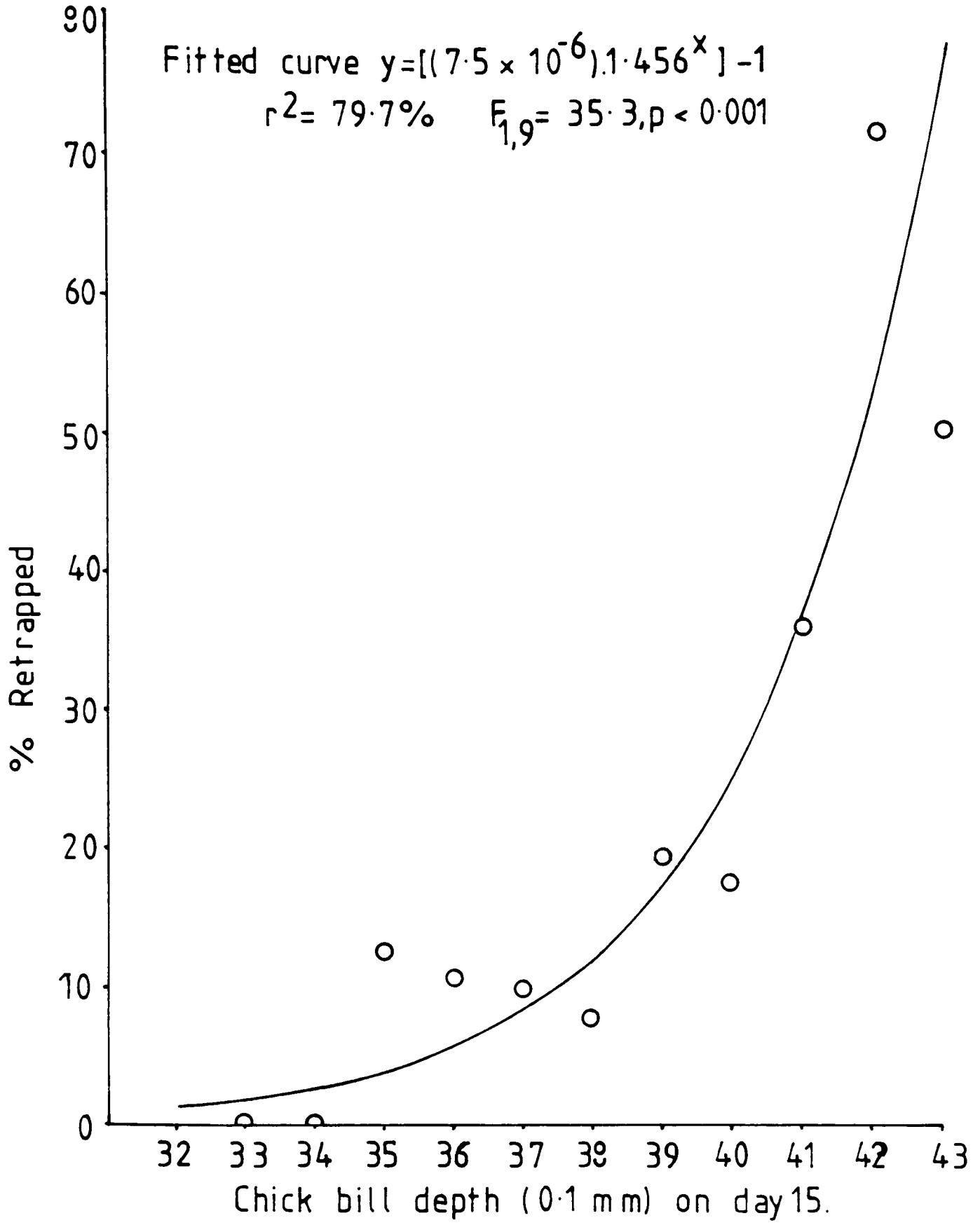


Figure 7.1. The 'apparent' relative fitness of bill depth classes based on 66 recaptures of 433 Great tit nestlings measured during the summer of 1984. This figure should be compared with Figure 7.2.

Table 7.6 The percentage of chicks in the 1984 cohort that were retrapped more than three months after fledging in the Wytham study area.

Weight class (g)	n.	rel.freq.	nº.retrapped	% retrapped.
14.Ø - 14.9	7	1.3	Ø	Ø
15.Ø - 15.9	14	2.5	1	7.1
16.Ø - 16.9	2Ø	3.6	1	5.Ø
17.Ø - 17.9	85	15.5	9	1Ø.5
18.Ø - 18.9	161	29.3	28	17.4
19.Ø - 19.9	161	29.3	41	25.5
2Ø.Ø - 2Ø.9	82	14.9	2Ø	24.4
21.Ø - 21.9	18	3.3	3	16.7
22.Ø - 22.9	2	Ø.4	1	5Ø.Ø

result is shown in figure 7.2. Clearly, bill depth was not the target for directional selection. Deep-billed individuals were selected indirectly as a result of their greater weight. However, the distribution was strongly bimodal, indicating disruptive selection for bill depth. Further, the disruption resulted partly through the differential selection of the sexes with respect to bill depth (sexed on recapture). In females, selection was strongly directional, favouring small-billed individuals. In males, selection was weakly directional favouring large-billed birds. Hence the results of selection were as presented in chapter 3 (i.e: males had significantly deeper bills than females).

Since the bimodality in the distribution shown in Figure 7.2 was due to differential directional selection of the sexes it is not, strictly, disruptive selection. Since the birds were not sexed in the nest, it is not possible to examine selection on the two sexes separately since the number of males and females in each nestling bill depth class is not known. To estimate when this differential selection acted, I repeated the analysis on data collected before the end of November 1984 (the median date for captures in that winter). Only one measured nestling was trapped before the end of October so that this was the earliest period for which such an analysis could be undertaken. The resulting distribution (n=33) represented in Table 7.7 was similarly bimodal, suggesting that selection had probably occurred by the end of November. Indeed, the poor correlation found between nestling and full-grown bill depths, suggests that disruption must occur very much earlier, before the bill is fully developed.

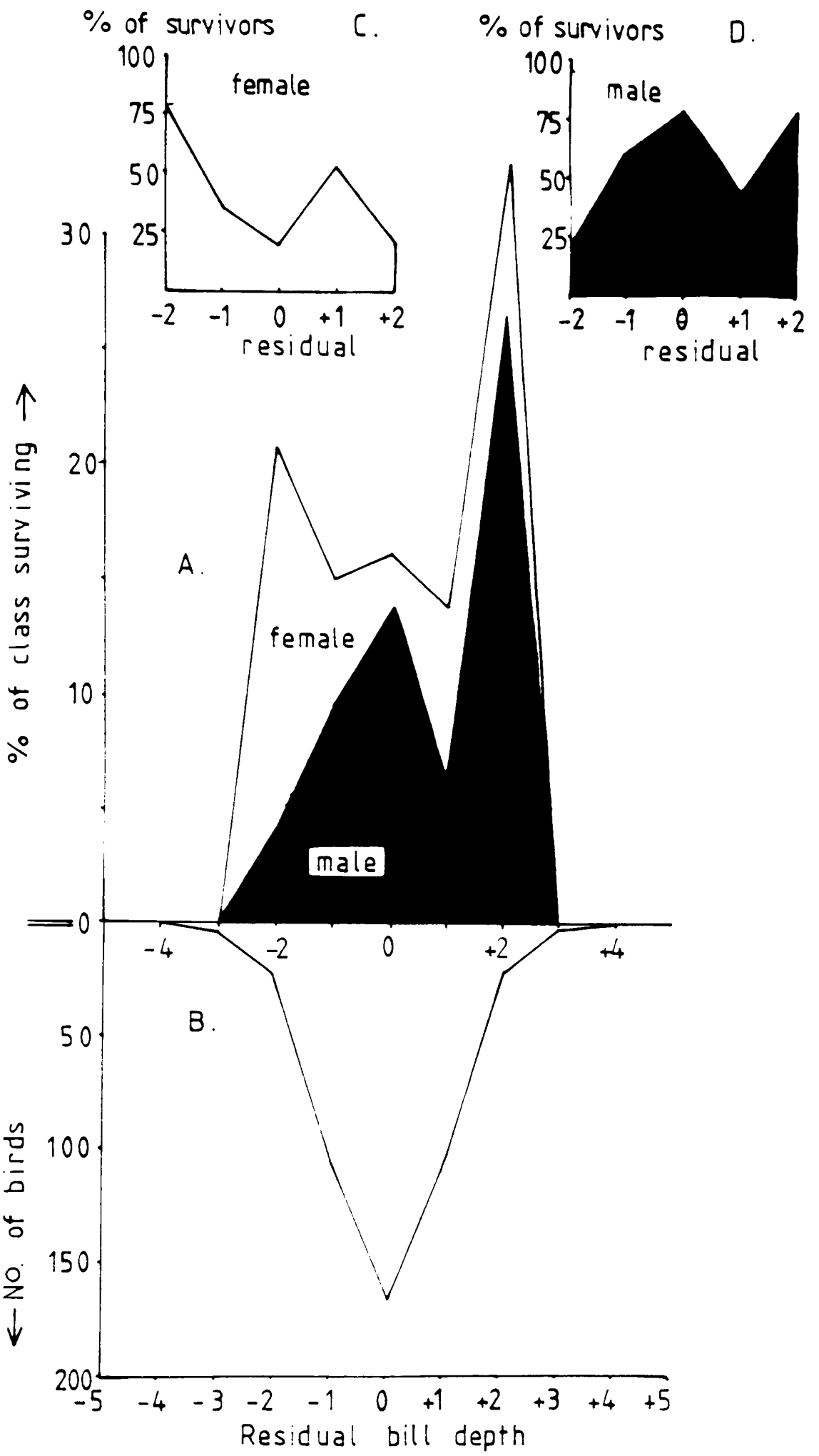


Figure 7.2. The relative fitness of bill depth classes (as Figure 7.1) after the removal of body weight (by regression analysis) as a confounding variable. Bill length categories (x axis) are therefore represented as residuals from the regression of bill depth on body weight (this regression analysis essentially gave the same linear equation for the whole sample (n=433) as for the retrapped sample (n=66)). The upper frequency polygon - labelled A, shows the whole percentage of the class retrapped. The percentage of each sex in that retrapped sample is then shown within this figure (females in white, males in black). Figures C and D above again show the percentage of the retraps ("survivors") that were female (C) and male (D). Figure B shows the frequency polygon of the original nestling distribution (n=433).

Table 7.7. Evidence that 'disruptive selection' acted on the 1984 cohort before the 30th of November 1984 (that is the median date of capture).

Residual bill depth of base population.	n.	nº.retrapped	% retrapped.	
-4	1	Ø	Ø	
-3	2	Ø	Ø	
-2	24	4	16.6	female mode
-1	105	7	6.7	
Ø	166	10	6.Ø	
1	109	7	6.4	
2	24	5	20.8	male mode
3	2	Ø	Ø	

7.5 Discussion

The results presented above (section 7.3) suggest that the selection of bill characters in adult Great tits occurred rarely during the study period. However, when observed, it was directional and usually favoured deeper-billed individuals. Hespenheide (1973) suggested that in seasonal, temperate environments, bill selection should be most intense in winter when food was most limiting. This was observed in the Wytham population. Of eighteen apparent cases of selection (directional and stabilising), only four were observed when summer data were taken as the base population. That selection was not observed in all status classes, or in all winters may reflect an 'ecological buffering' of individuals through phenotypic plasticity. That is, since individuals could, to some extent, alter their morphology in response to a changing trophic environment, mortality due to maladaptive morphology is reduced. This view is supported by the observation that adult males (the most dominant social class) were never selected differentially on bill size. These birds were buffered both socially and morphologically.

Section 7.4 gives the strongest evidence for the selection, and therefore adaptive significance, of a bill character. It is not clear from these data, to what extent the sexual dimorphism observed in the Wytham population (when full-grown) may be attributed to differential selection acting in opposite directions on the two sexes during the three months after fledging. If sexual dimorphism results partly from such selection, there is no a priori expectation for sexual dimorphism in bill characters in all populations. Further, if sexual dimorphism is caused by such differential selection acting due to differential niche-occupancy by the two sexes resulting from intraspecific competition, and if the intensity of competition amongst

fledglings is a function of their density and date of fledging (as argued by Dhondt 1979, Dhondt & Olaerts 1981, and Drent 1983), then the degree of sexual dimorphism might be predicted for a given population from a knowledge of these parameters. Although this is mere speculation, it is consistent with Van Balen's (1967) observation that sex and age differences in morphological characters varied among populations (see introduction).

Disruptive selection for bill characters has been described rarely (Endler 1986). Grant (1985) showed a tendency toward 'disruption' in Geospiza conirostris. Here, it resulted because the sexes showed different adaptive peaks. It was therefore, not strictly disruption but due to differential selection of the sexes as shown in the Great tit. Similarly, Schluter & Smith (1986) found differential selection on bill characters of the Song sparrow Melospiza melodia. Here again, 'disruption' was caused by differential selection of the sexes. Selection on males was weak and stabilising, on females - was strong and both directional and stabilising. In Geospiza, selection usually acted most intensely on bill depth (Boag & Grant 1981, Grant 1985, Schluter et al. 1985) since seed-size was the agent of selection. In Melospiza selection was most intense on bill length as habitat constraints were probably the agents of selection (Schluter & Smith 1986).

Chapter 8. Final discussion and conclusions

"We suggest that morphology can be a powerful tool in the analysis of community structure."

Ricklefs & Travis, 1980.

Chapter 8. Final discussion and conclusions.

8.1. Synthesis.

This chapter attempts to consolidate the results of this study, considering them in the context of the ecological principles introduced in chapter 1. A principal finding of this study has been the relative importance of immediate environment in determining the phenotypic variance in bill characters. The relationship between bill index and the rate of food handling indicated the general importance of bill size (section 4.3), and predicted that seasonal, age and sex differences in bill size might be expected if the variation in bill size co-varied closely with variation in the niche within or between members of the population.

The extent to which bill variation was determined by sex- or age-differences, itself varied strongly between seasons. This resulted from clear seasonal differences in the fundamental (or available) and realised niches (see chapter 4). For example, in winter, age- and sex-specific differences in bill depth varied in response to the availability of beech mast, and in summer, there was some evidence for a habitat effect on bill length (see chapter 6). Further, differences in the relative importance of the environmental component of phenotypic variance had a marked effect on the estimated degree of heritability of bill characters. Several other lines of evidence further supported the assertion that the environmental influence on bill variation was greater in winter than summer. For example, the correlation between bill length and depth (which was highly significant in the skeletal measurements) was noted mostly in summer rather than winter (see especially chapter 3). I shall argue that these differences resulted largely

from the seasonal change in the social organisation of the population.

Evidence for the adaptiveness (defined in chapter 4) of bill characters was demonstrated in both winter (chapter 4) and summer (chapter 5), but it was suggested that the adaptive significance of specific characters differed between these seasons. For example, in winter (autumn and spring) bill depth was sexually dimorphic more often than bill length. Bill depth was significantly correlated with body weight more often when the birds were feeding on beechmast than when they were not (see chapters 3, 4 and appendix 2), and I suggested that this might reflect the feeding efficiency of the different birds in relation to their bill size. Further, although evidence for natural selection of bill characters was rarely observed in adults, when it occurred, it was observed more often in winter than summer, and it tended to favour a shorter, deeper bill. Hence bill size was probably of direct importance to the individual. In summer bill length was sexually dimorphic more often than bill depth, and there was no obvious pattern to the occurrence of correlations between bill size and body weight (appendix 2). The adaptive significance of an adult Great tit's bill length in summer probably lay more in its relation to fledging weight and survival of the offspring than to its own survival (chapter 5). Hence adult survival was probably not related to bill size and so there was little evidence for the selection of bill characters in summer.

The underlying causes of these seasonal differences are the relative abundance, type and distribution of available food. This causes a shift in both the fundamental niche (from an invertebrate to a seed diet) and the social organisation of the population (from territoriality to the formation of flocks and/or aggregates). Krebs et al. (1972) and Krebs (1973) showed that flock formation in tits was itself adaptive since individuals gained

information about the distribution of food from other members of the flock. Baker (1978) pointed out that the advantages to an individual bird of joining a flock differed among status classes since (as Gibb (1954) had shown) the shift to flock or aggregated foraging, leads to an elevated degree of direct intraspecific competition (manifested in an increased frequency of supplanting attacks) and the establishment of a dominance hierarchy. Glase (1973) showed that in the Black-capped Chickadee Parus atricapillus, such a linear dominance hierarchy was the principal cause of differential age- and sex-specific niche occupancy. He showed that males always dominated females, and that within the sexes, older birds always dominated younger individuals. A linear hierarchy of this nature has also been demonstrated in the Great tit (Hinde 1952, Garnett 1976, Drent 1983). Hence dominance relationships within observed flocks may be predicted and intraspecific variation in niche occupancy may be attributed reasonably to such dominance interactions (although further research may be required to demonstrate conclusively the nature of this relationship).

In the present study, intraspecific variation in the niche was most clearly observed between the sexes (since niche variation in relation to age could not be determined in the field). Sex differences in foraging niche have been described in a wide range of species, from raptors (Newton 1979) to Dendroica warblers (Morse 1968).

In the Downy Woodpecker Picoides pubescens, Peters & Grubb (1983) showed that differential niche occupancy by the sexes was caused by direct interference competition. If males were temporarily removed from the territory, females expanded their realised niche to include the exclusive male niche-space from which they had previously been excluded. In the Great tit, females occupied a broader niche than males. Table 8.1 shows the

Table 8.1. Sex differences in niche breadth observed in foraging Great tit flocks in winter. Niche breadth is given as the Shannon-Weiner diversity statistic $\bar{H}$ calculated using the formula given in chapter 5 where p_i is the probability that an observation drawn at random will fall in the ith category of height or feeding method respectively. The data used were presented in Table 4.2 and Figure 4.2. The height categories used were shown in Figure 4.1 and the feeding method categories (hammering, probing or gleening) were shown in Figure 4.2.

Diversity of foraging ($\bar{H}$).

	Feeding height.		Feeding method.	
Winter.	male.	female.	male.	female.
1982/83	1.251	1.572	Ø.311	1.Ø99
1983/84	1.Ø84	1.179	Ø.188	Ø.225
1984/85	1.246	1.551	Ø.227	Ø.378

diversity (calculated as $\bar{H}$ values) in the niches occupied by each sex along two niche dimensions (feeding height and method) in each winter. Methods and further details on the collection of data for this analysis were given in Chapter 4. In each case, females (the subdominant sex) occupied a relatively broader niche than males. This pattern was also found in the comparison of prey types in the winter of 1984/85 (Table 4.3).

Sex differences in foraging niche are not always caused by direct competition between the sexes. In raptors, sexual dimorphism in body size results in a difference in the mean size of prey taken. Body size dimorphism may itself have resulted from character displacement acting to reduce competition. However, niche differences are maintained by the difference in morphology, and not by the presence of a competing mate. It is not clear whether sexual selection could be responsible for this dimorphism since females usually exceed males in body size in the Falconiformes (Amadon 1959, Mueller & Meyer 1985). Morse (1968) found that in several Dendroica species of the North American Spruce woods, males fed at a significantly greater height than females in summer. He suggested that, rather than functioning to reduce niche overlap within the pair, this was simply because males generally sang from high perches, and they foraged at that height, whilst females foraged at the lower level of the nest. I shall return to the question of niche variation in section 8.3.

The relationship between niche differentiation and sexual dimorphism was introduced in chapter 4. In the Great tit in winter, sex differences were observed in the length and depth of the bill, in the amount of abrasion on the culmen, in the incidence of bill moult, in the curvature of the culmen and in the correlation between bill shape and length. Table 3.25 showed that in males, a shorter bill corresponded to a more rounded culmen (a negative

correlation), whilst in females, a straighter bill tended to be shorter (a positive correlation). This suggests a fundamental difference in the size/shape relationships of the bill in the two sexes which are independent of allometric scaling effects. Sexual dimorphism was observed in both the size and shape of the winter bill.

In chapter 1 I criticised much of the previous work in avian community ecology for assuming (without empirical evidence) that bill size and prey size were correlated. I have shown that bill length in the Great tit may co-vary with prey size, but that the relationship is negative (Figure 5.3). Many studies (see Table 4.1) have suggested that in addition to (or indeed instead of) this relationship, the variance in prey size increases with an increase in bill length. To test whether this was true for the Great tit, I plotted the coefficient of variation in prey size against the parental bill length for the eight broods used in Figure 5.3 (in which the parental bill-difference was less than 0.2 mm). This is shown in Figure 8.1. As predicted, prey-variation and bill length were significantly and positively correlated.

Schoener's (1971) model of foraging strategies predicted that when food was super-abundant (high encounter rate), individuals should specialise on the optimal prey type. For this model to function, the birds must be able to make a distinction between prey items which may differ by a relatively small amount. Several workers have reported on the strong discriminating abilities and high degree of food selectivity exhibited by the Great Tit (Tinbergen 1960, Mook et al. 1960). Vince & Warren (1963) found that Great tits learnt quickly to discriminate by taste and that older, more experienced birds were more selective than younger birds. Gibb (1960) showed that invertebrate food

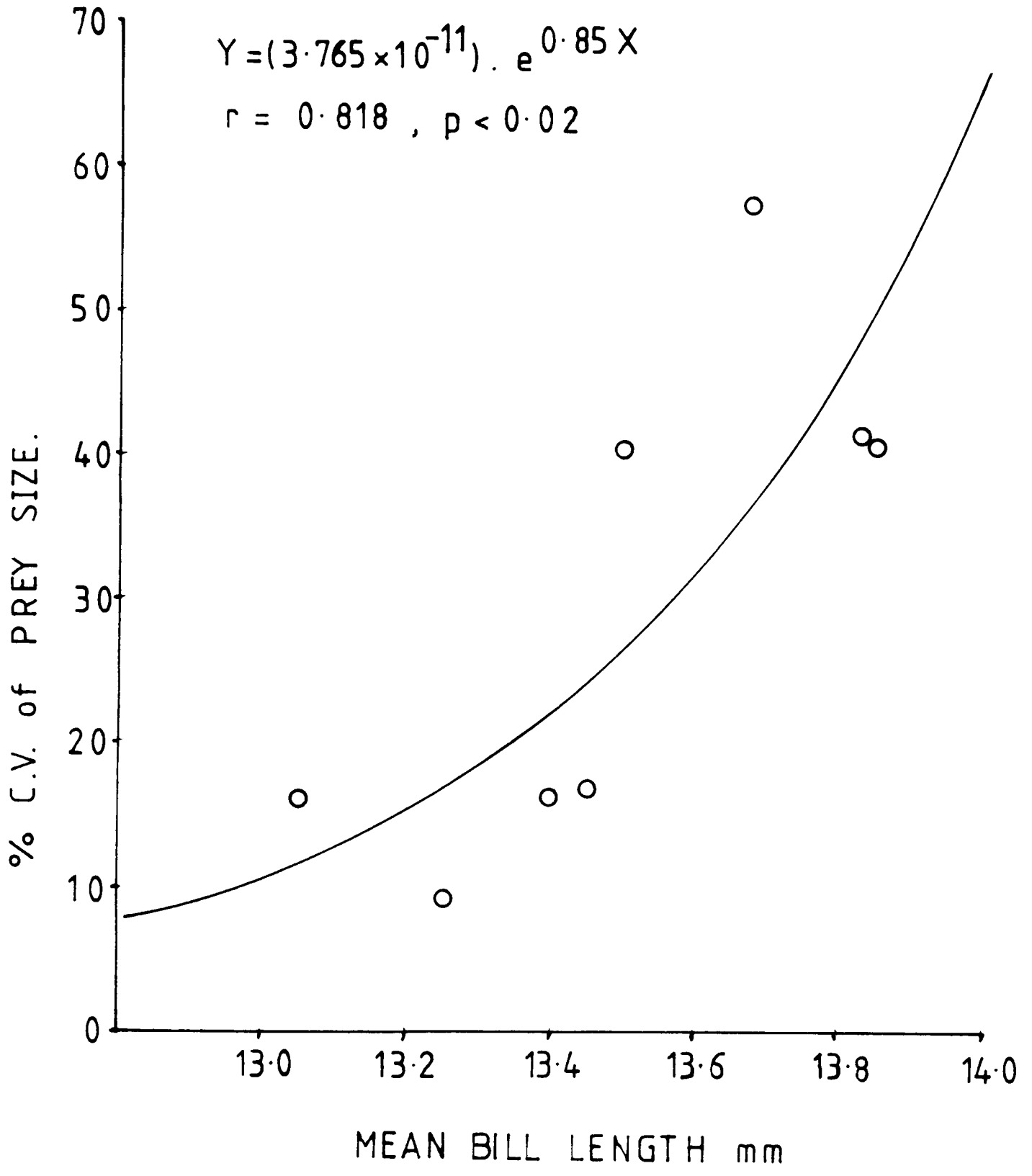


Figure 8.1. The relationship between the relative variation in prey size (c.v) delivered to eight nests in 1984 and the mid-parent mean bill length of the parents. Only nests in which the parental difference in bill length was less than 0.2mm were used. The figure should be compared with figure 5.3 which was drawn from data collected at the same nests. The linear function Y=-625+4.85X was also significant, r=0.769, P<0.05.

in woodland was distributed patchily, and Smith & Dawkins (1971) found that Great tits showed a strong preference for feeding in the most profitable patches. In the Great tit, the general prediction of the Schoener model (reported above) has been supported by a number of laboratory studies (Smith & Dawkins 1971, Houston et al. 1980).

In chapter 5. I showed that bill length and prey size were not always correlated in summer. I suggested that this might reflect differences in the foraging strategy of the parents in response to variation in prey abundance in accordance with Schoener's model. Hence in some years, prey selection was made partly on the basis of bill length, but in other years was not. Although feeding conditions differed in the two summers compared (1984 and 1985), there was no significant difference in the mean fledging weights of chicks. This is to be expected if the foraging strategy employed was itself adaptive, enabling the parents to maximise the rate of food delivery to the nest. Chicks would then be buffered effectively against variation in food abundance by the behavioural plasticity of their parents. This would also give an under-estimation of the importance of bill length (or bill length difference between parents) to the fledging weights of chicks. Hence the low apparent covariance between parental bill-difference and fledging weight presented in chapter 5, although statistically significant, may be an under-estimate.

In the next section (8.2) I shall consider the parallels observed in this study between intraspecific bill variation in the Great tit, and the general model of character displacement described in chapter 1. I shall then return to the relationship between niche variation among age and sex classes (section 8.3). Finally (section 8.4), I shall attempt to incorporate all of these results into a simple model relating bill morphology to ecology in the Great tit population at Wytham.

8.2. Character displacement.

Ricklefs & Travis (1980) described character displacement as a mechanism allowing fine tuning of a community, thus allowing subtle adjustments of specific niche-space by corresponding adjustments in morphological space.

The models developed by Smith et al. (1978) and Cody (1973) (described in chapter 1) and combined in Figure 1.1 make simple and general predictions of the response of morphological variation and foraging strategy to changes in food abundance. The validity of the models may be tested (to some extent) by reference to intraspecific variation in morphology and the niche-space. The models predicted that character displacement should occur under conditions of very high and very low food abundance. When food was moderately abundant, character convergence should occur. The present study gives general (though weak) support to this model. In the study of intraspecific variation, sexual dimorphism is considered to be analogous to character displacement between species. In summer, when food is relatively super-abundant, divergence in bill length between sexes was observed. Since phenotypic variation in the summer is believed to reflect the underlying genetic variation most closely (chapter 3), it may represent true character displacement by under-utilisation as described by Hespenheide (1973) (see chapters 1 & 5). In spring when food was generally least abundant (Elton 1966 and chapter 2), most character divergence was observed. Divergence occurred in both bill length and depth, between sexes (in bill depth), and in males also between age-classes (in bill length). In autumn, when food was moderately abundant, age-specific variation in bill length and depth was not observed. However, sexual dimorphism was observed and this was at least as strong an affect as in summer. Since the relative positions of these seasons (autumn, spring, summer) on the

food abundance axis of Figure 1.1 cannot be determined, the true correspondence between the model and these data cannot be ascertained.

Although these results follow broadly the predictions of the model, it must be remembered that, to some extent, the observations concern phenotypic changes within individuals (especially in winter), that is, variation within the environmental component of phenotypic variation. This is quite different from the usual formulation of the "character shift" concept which concerns changes within the genetic component resulting from the differential fitness of morphs and therefore, differential directional or stabilising natural selection. Hence intraspecific variation offers for study a situation which might parallel that of the interspecific case without being exactly comparable.

Hogstad (1978) has pointed out that it is in the nature of winter niche-shifts in Parus that it occurs as an "immediate and variable response to the prevailing incidence of interspecific competition". This suggests that it is not under genetic control. In chapter 1 I introduced the terms "behavioural" and "selective" to describe two rather different types of niche shift. A behavioural niche shift results from direct interference competition for food and is typified by the Downy Woodpecker example described above (Peters & Grubb 1983). The selective niche shift results from either direct or diffuse competition and involves natural selection for differences in niche occupancy between competitors (see section 1.2). The niche differentiation observed in the Great tit in winter is of type 1 (behavioural shift). This is indicated partly by the differences between winters and sites in the degree to which the sexes themselves differed in niche occupancy (Table 4.2). The niche shift observed between members of a pair in summer would constitute a selective shift (type 2). In parallel with this distinction, we might

distinguish between two types of character displacement. Character displacement affecting the environmental component of phenotypic variation might be termed "Environmental character displacement". This arises from phenotypic plasticity in response to a behavioural niche shift and therefore results from direct interference competition. By contrast, character displacement affecting the genetic component of phenotypic variation might be termed "Genetic character displacement". This arises from differential natural selection as described by Grant (1972) in response to a selective niche shift and might therefore result from either diffuse or sustained direct competition. This distinction is summarised as follows:

Character displacement:	"Genetic"	"Environmental"
Competition:	Direct or diffuse	Direct.
Niche shift:	"Selective"	"Behavioural".
Component of phenotypic variation:	Genetic	Environmental.

It might be noted also that in the Great tit, the niche dimensions involved in these contrasted types of niche shift may be quite different. In summer, niche segregation probably occurs only along a dimension of prey size. In winter, food type (mast or invertebrates), feeding location and feeding method are all involved.

The relationship between character displacement or convergence and food abundance is intimately related to the question of dietary specialisation or generalisation which was considered briefly in the last section. In its simplest form (as Figure 1.1), this was not borne out by the present study since intraspecific dominance relationships - superimposed on the general

pattern - influence differentially the availability of food (realised food availability) to different status classes within the population.

Hamilton & Johnston (1978) argued that the degree of age- or sex-specific differentiation in trophic characters within a population, reflects a balance between the levels of interspecific and intraspecific competition. They suggested that interspecific competition should tend to reduce the specific realised niche breadth and that this would reduce the specific variance of relevant trophic characters. Intraspecific competition, on the other hand, should tend to increase the specific realised niche breadth (total niche breadth of the population) as age- and sex-classes diverged in niche, and consequently in morphology also. Although both inter- and intraspecific competition may vary between seasons, the mean niche-breadth and morphological variance should ultimately reflect the mean levels of the two processes. Rothstein (1973) used a similar argument in his defence of the Variable Niche Hypothesis (see chapter 1.). However, the observed relationship between these variables will depend upon the fundamental niche-volume which is not occupied by competitors (vacant space). High levels of both inter- and intraspecific competition may act simultaneously, the former reduces niche breadth relative to other species, whilst the latter still acts to increase the class-specific (age or sex) niche breadth - possibly along new niche dimensions - within a species.

In reality and with regard to their respective forms of character displacement, whilst both inter- and intraspecific competition in Parus may be either diffuse or direct, interspecific competition for food in summer is more likely to be diffuse and may be reciprocal. In winter it may be both diffuse or direct, but the Great tit is always (more or less) dominant in direct interactions. Intraspecific competition for food is probably most

important in winter and is more noticeably direct (than interspecific). It is rarely reciprocal because individuals of a species competing directly for resources are rarely equivalent due to the influence of dominance interactions (Begon & Mortimer, 1986). Hence inter- and intraspecific competition may act in different ways, mediated by different behavioural or ecological mechanisms and acting upon different components of the phenotypic variation in morphological characters in different seasons. I shall return to this in section 8.4.

8.3. The "Variable Niche Hypothesis".

The "Variable Niche" or "Niche Variation" hypothesis propounded by Van Valen (1965) states that when the intraspecific realised niche-space of a species is sub-divided predictably among infraspecific classes or status groups (eg: by age or sex), an increase in the total specific morphological variance might result. This pre-supposes that niche subdivision occurs by differential niche specialisation by these classes within the specific niche volume (Van Valen & Grant, 1970). It is assumed also that such divergence in infraspecific niche-space results from intra-specific competition (Hamilton & Johnston 1978, Rothstein 1973) and that interspecific competition does not limit the expansion of the total specific niche-volume. In its simplest formulation, the variable niche hypothesis states that morphological variance is some positive function of niche breadth.

Sasvari (1979) found that the Great tit was the most behaviourally adaptable of several Parus species studied and suggested that this was reflected in the expanded niche-space shown by the species as a whole (see section 1.3). In the Great tit (socially dominant among the British Parus), interspecific competition for food in summer is of a diffuse rather than a direct nature (see chapter 1.). In winter, it may be directly influenced more by intra- than interspecific competition and exhibits a well established dominance hierarchy. Hence of the six British Parus species, it is the most suitable species to test the variable niche hypothesis.

The intraspecific formulation of the variable niche hypothesis considers niche breadth as a function of the gradient in foraging strategy from specialist to generalist. Morse (1971, 1974, 1980) developed the argument of Levins (1968), suggesting that socially dominant classes of a species would

be more specialised in their foraging than subdominant classes. This was because dominant individuals had greater access to food than subdominants and therefore food was relatively more abundant for them. Hence when a dominant class was able to monopolise a resource, it would do so and specialise upon it. Subdominant classes were forced to employ a more opportunistic or generalist foraging strategy (see also Baker 1978). The morphological formulation of this reasoning is as follows:

Status class:	Dominant	Subdominant
Relative foraging strategy:	Specialist	Generalist.
Relative niche breadth:	Narrow	Broad.
Relative morphological Variance:	Low	High.

It will be recalled from Table 8.1. that the niche breadth occupied by males (dominant sex) was indeed narrower than that shown by females (subdominant). The relative morphological variance may be expressed either as the coefficient of variation, or as the standard deviation of the log transformed values of a character (in which the variances are standardised relative to the means - homoscedastic). In the Great tit the ranked order of these measures of relative variation of bill index taken across all winters is given in Table 8.2. The rank order was as predicted by the hypothesis. Males differed significantly from females when age-classes were combined within sexes ($F_{429,508}=1.377$, $P<0.05$). First-year females did not differ significantly from adult females, nor did either female class differ significantly from first-year males. However, the difference between adult and first- year males was highly significant ($F_{298,211}=1.385$, $P<0.01$), as

Table 8.2. The relative variation in bill index of each age- and sex-class of all Great tits handled at Wytham during the winters of 1982/83 - 1984/85. The table gives the sample sizes (n), the coefficients of variation of the character (c), the standard deviation of the log tranfsformed data (Ln s) and the range of least significant difference (LSD) for this standard deviation.

Age	Sex	n	c	Ln s	LSD
Adult	male	212	3.68%	Ø.Ø383	Ø.Ø329 - Ø.Ø445
1Y.	male	299	4.37%	Ø.Ø459	Ø.Ø395 - Ø.Ø533
Adult	female	15Ø	4.86%	Ø.Ø5Ø1	Ø.Ø431 - Ø.Ø582
1Y	female	28Ø	4.87%	Ø.Ø524	Ø.Ø451 - Ø.Ø6Ø9

The LSD stated is the range within which another standard deviation would not differ significantly at a probability of Ø.Ø5 assuming that its variance ratio was calculated with degrees of freedom 12Ø,12Ø ($F_{12Ø,12Ø}$=1.35). In reality, most sample sizes were considerably greater than this and so the standard deviations may differ at a greater level of statistical significance.

was the difference between adult males and both female classes (see Table 8.2).

Further consideration of the variable niche hypothesis suggests that the separation of class-specific (age and sex) niche spaces and morphological differentiation should be most pronounced when food was least abundant. To test this I repeated the analysis of relative variation shown above (using the standard deviations of Log_e Bill index), but divided the data into seasons with good and poor beech crops (on or off mast in chapters 3, 4 and Appendix 2). Figure 8.2 shows the relationship between the relative variation in bill index in each status class under the two levels of food abundance. It should be pointed out that the status scale (x) in Figure 8.2 is an ordinal scale. Therefore it might not present the correct relative positions of the classes. Hence the true relationship between status and the relative variation in bill index might be curvilinear, and this might affect the significance of the correlation between them.

Figure 8.2 suggests that when little beechmast was available, a significant increase in the relative variance in bill index was observed in the subdominant classes. The rank order of bill variation was in accord with the hypothetical predictions (although the sex difference was far greater than the difference between age classes within each sex) and the difference between adult males and first-year females was highly significant ($F_{99,74}=2.42$, $P<0.001$). However, when beechmast was abundant, no significant difference in bill variation was observed among classes. Therefore it may be supposed that when mast was abundant, all were able to specialise on the preferred food and the mean variance in bill index was comparable with that of the most specialised class (adult males) under conditions of low food abundance. The low relative variation in bill index of the dominant classes

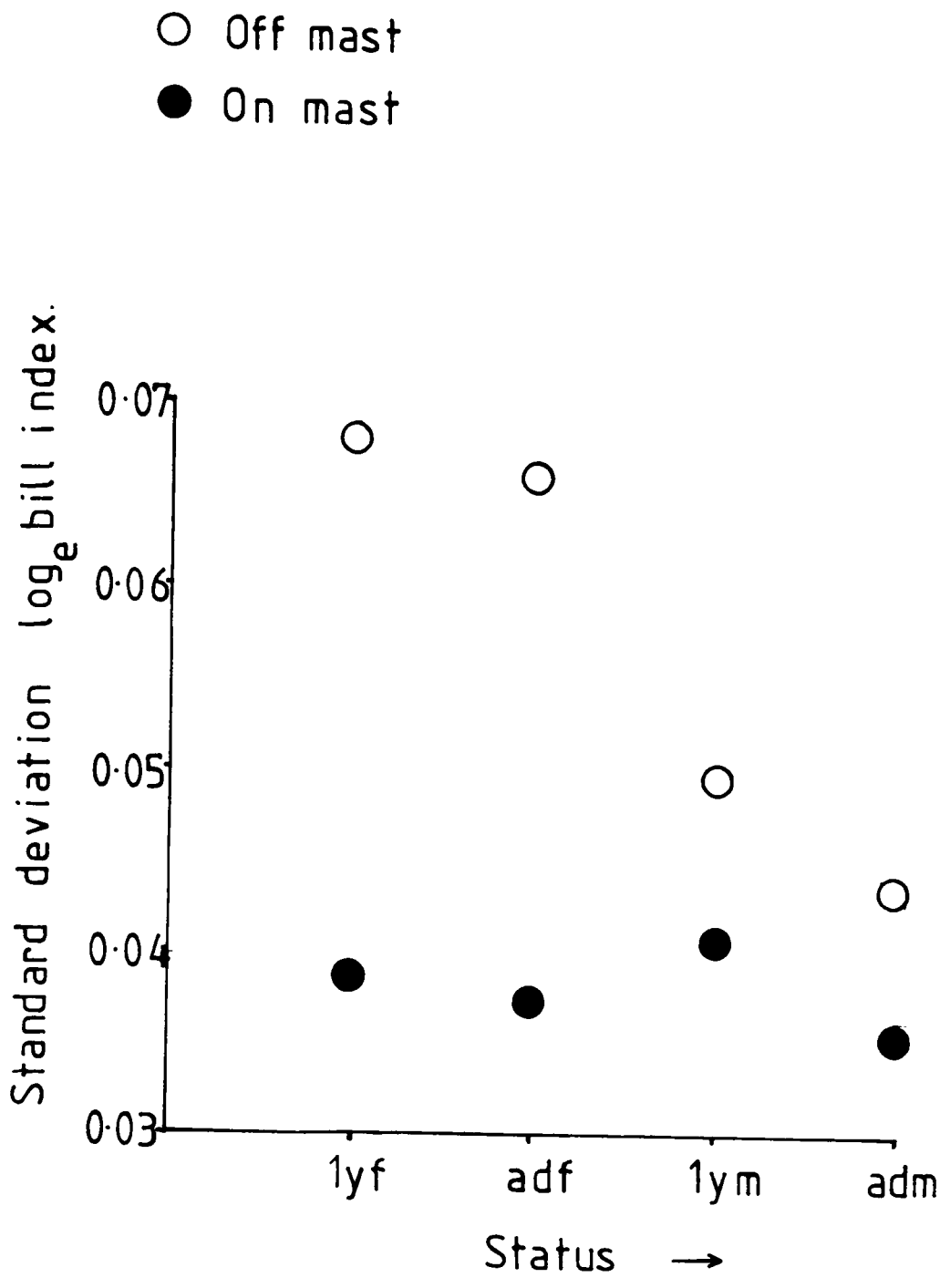
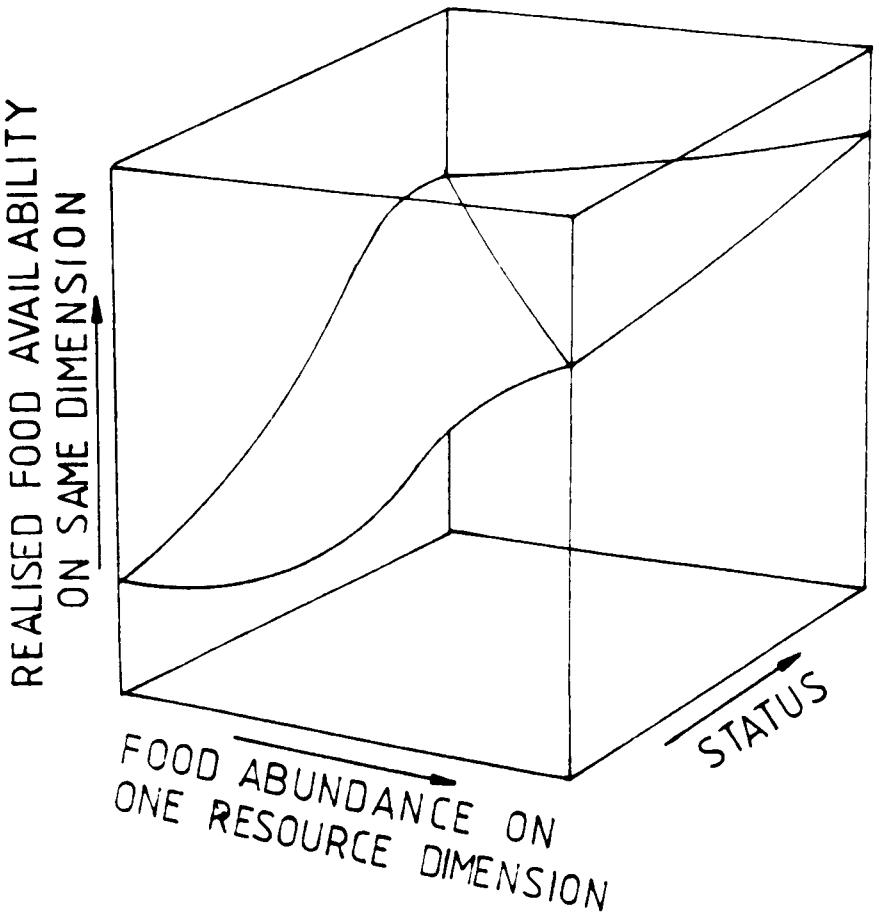


Figure 8.2. The relationship between the relative variation in bill index (as s.d. log$_e$ bill index) and the relative status of the class of birds under conditions of relatively high food abundance (filled circles) and relatively low food abundance (open circles) indicated by beech crop data. The differences between male and female classes when food was scarce, was higly significant (see text). The graphs show that when food was abundant there was no significant difference between classes in the within-class variation of bill index. When food was relatively scarce, the variation among dominants was significantly less than that of sub-dominants as predicted by the variable niche hypothesis.

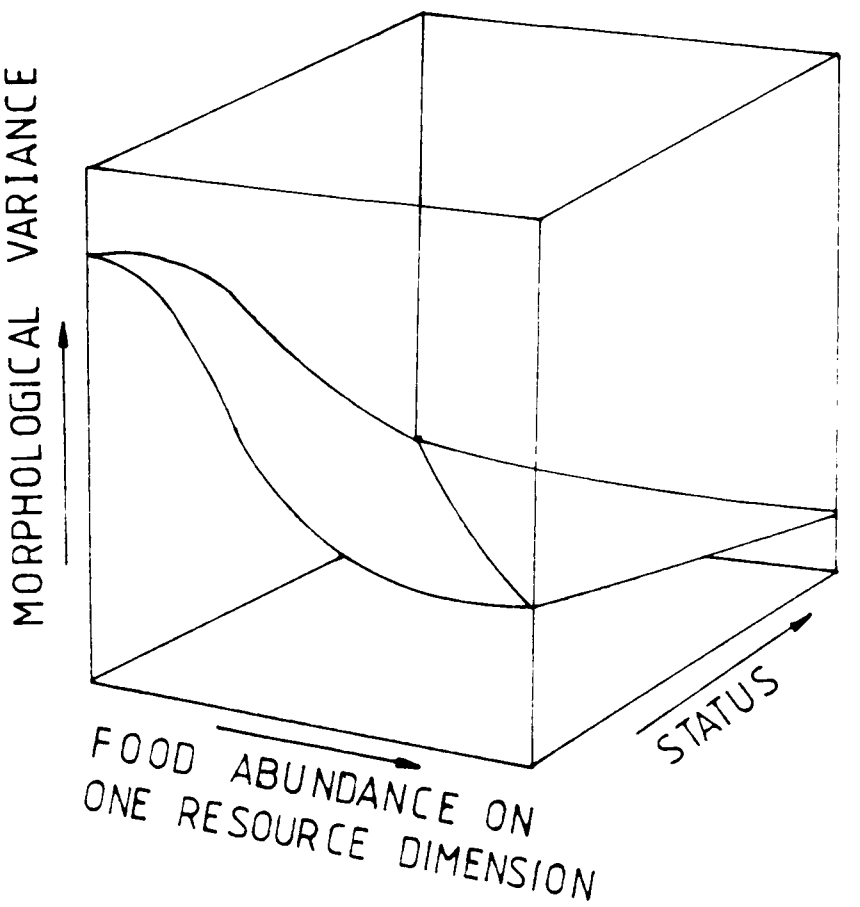
could result from a morphological convergence of individuals toward some optimal bill size determined by the favoured resource upon which specialisation occurred (beechmast). The relatively high variation among sub-dominant individuals may have several causes. It may simply reflect the "unspecialised" level of variation, or it may be due to differential micro-niche specialisation among members of the sub-dominant classes.

This provides strong evidence in support of the variable niche hypothesis. Figure 8.3A summarises diagramatically, the relationships between the actual food availability on a given resource dimension, and the realised food availability on that dimension in the presence of competing conspecifics. Figure 8.3B summarises the morphological corollary of this in similar form. This is a graphical representation of the Variable Niche hypothesis as it applies to intraspecific competition.

Finally, it might be added that the lack of age-specific bill variation in summer might also be predicted by the variable niche hypothesis since once territories have been set up, they impose a different pattern of intraspecific competition in summer, in which age-related dominance mechanisms are inapplicable.



A.



B.

Figure 8.3. Schematic representation of the intraspecific formulation of the "variable niche hypothesis". Figure A (above) shows the change in food availability (in real terms) to different status groups with a change in food abundance along the same resource dimension. Figure B (below) shows the morphological corollary of this in terms of the change in relative variation in trophic characters in different status classes with the same change in resource abundance.

8.4. Morphological variation as a function of social dominance.

I have shown that female Great tits foraged within a relatively expanded niche in winter, and I suggested that this was related to their dominance rank in the manner described by Morse (1974). In a somewhat different context, Klopfer & MacArthur (1960) argued that niche breadth could be described as a function of behavioural plasticity (opportunism in the present context). Hence by inference, subdominant individuals may be more opportunistic than dominants. This does not imply that there are genetic differences between status classes which predispose them differently in their behaviour. It may mean simply that (possibly out of necessity) subdominants may be more willing than dominants to exploit new situations. In some respects, this has already been demonstrated in the Great tit. Krebs (1971) showed that first-year male Great tits were significantly more likely to desert a territory in sub-optimal habitat than were adult males in the same poor habitat (hedgerow) when a vacant territory bacame available in a better habitat (Oak woodland).

The results presented strongly support the arguments of Snow (1954) and Lack (1971) on niche segregation and competitive exclusion, and of Levins (1968) and Morse (1974, 1980) on the role of social dominance in mediating the niche-morphology complex. Patterns of interspecific variation in Parus are paralleled within the species. Hence for example, thin-billed (female) Great tits fed higher than deep-billed (male) Great tits (chapter 4), and this corresponded to a difference in the proportion of invertebrate prey in the diet, as generally described in Parus by Snow (1954). In winter, social dominance is regarded as the principal agent of ecological segregation

leading (through phenotypic plasticity and a close tracking of niche changes by morphology) to the intensification of existing sex differences in bill morphology. As described above, this is analogous to character displacement (sensu Grant 1972), but within the lifetime of the individual following niche segregation by direct interference competition as demonstrated by Peters & Grubb (1983).

The system may be regarded in terms of a simple bivariate model (Figure 8.4) in which variation in parameters of the niche-morphology complex are related to the dominance rank of a class by a positively accelerating curve. Since variation in the niche-space and morphological-space (sensu Hutchinson 1957, and Ricklefs & Travis 1980, respectively) are highly correlated, in reality, they might be represented by PC1 derived by a Principal Components Analysis of the combined ecological and morphological matrices (eg: Ricklefs & Travis 1980). From Figure 8.4 it will be seen that both female classes lie close together on the morphological axis whilst the male classes, with increasing dominance, separate more from the females and from each other. This model predicts the observation of age-specific bill-variation in males but not females. It predicts that more of the correlation between bill depth and body weight should be due to body Size in males than in females. It also explains why the coefficients of variation in bill index (across all winters) were essentially the same in both female classes but differed significantly in males.

Myton & Ficken (1967) studied the seed-size preferences of Tufted tits Parus bicolor and Carolina chickadees P. carolinensis. They found that the larger Tufted tits always selected the larger seeds. Below 0^{o}c and in the presence of the dominant Tufted tits, the chickadees were not selective, although when not so stressed, they also always preferred the larger seeds.

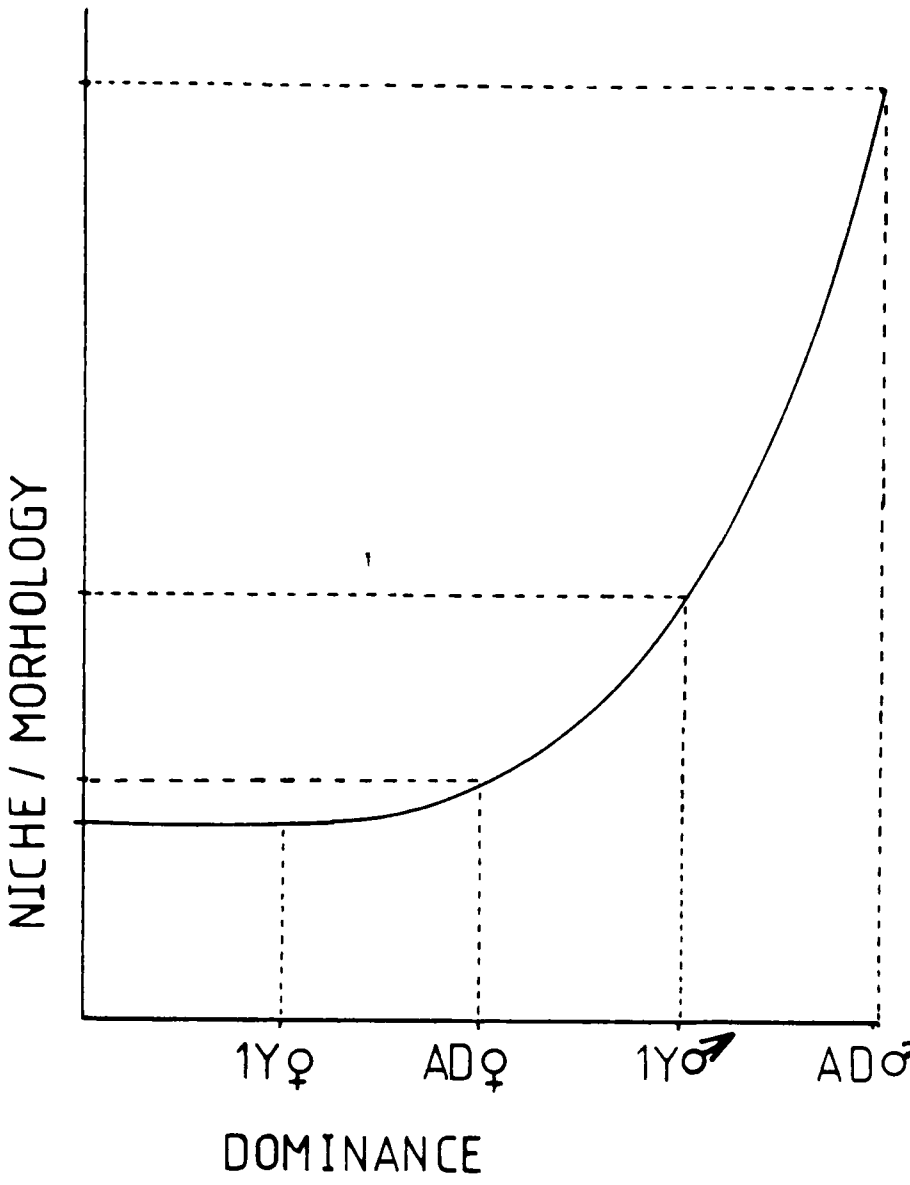


Figure 8.4. A simple bivariate model relating the niche/morphology complex (y) to an index of relative dominance status (x). In the model, status classes are shown to be equally separated along the dominance gradient (as Figure 8.2). The Y axis shows increasing differences between classes in variables of the niche/morphology complex with an increase in dominance. See text for further explanation.

Although much criticism may be levelled at their experimental design (for example: the birds were not ringed and so there is no evidence that the birds present under different conditions were the same), their suggestion that the presence of a relationship between bill-size and seed-size depended upon the degree of environmental stress (climatic or social) was important. The results presented in Figure 8.2 also strongly support the view that morphological/niche relationships vary with the degree of stress.

The intervention of dominance in determining an individual's access to resources causes a reversal in the relationship between food availability and the foraging strategy expected from Figure 1.1. That model predicted that when food was very scarce, individuals should specialise. Morse (1980) has argued that subdominants, whose resources are scarcer than dominants, should generalise their foraging (see Figure 8.3). However, the model described by Smith et al. (1978) (Fig. 1.1) was concerned with interspecific competition in which it is assumed that foraging becomes relatively more specialised as a result of a narrowing in the realised niche breadth and character displacement in the presence of a competing species. It is, therefore, not directly applicable to the intraspecific case.

Two consequences of subdominance and direct competitive exclusion for female Great tits may be their reduced breeding-site fidelity and tendency to travel greater distances between natal and first breeding site (Harvey et al. 1979, Dhondt 1979). This relationship was indicated by the emigration of subdominant (and especially female) Great tits from Wytham during the winter of 1983/84 described in chapter 4. These factors undoubtedly contribute to the greater mortality of females that has been noted in several populations (Bulmer & Perrins 1973, Orell et al. 1979, Clobert et al. in prep., Dhondt 1970).

In this study, I have suggested that the patterns of morphological variation observed in a population result partly from the interplay of natural selection (sexual dimorphism in first-winter Great tits might have arisen by differential selection - see chapter 7) and social behaviour (through the mediary of niche segregation). These are clearly effects which might be specific to a given population. The intensity of selection itself, the characters selected and the direction of selection may all relate to differences in population parameters such as the density and survival rates of the birds, and the avalability, type and distribution of food. The greatest differences in these parameters are observed between habitat types such as coniferous and deciduous woodland or at different latitudes. Hence, with a greater understanding of the processes operating within populations, we should now re-assess these relationships among populations and especially under different environmental conditions.

Plates

Plate 1. Photographic apparatus described in chapter 2. The design consists of a 'Cosina' CT-1G SLR camera fitted with a 'Macro' close-up lens and a 'Starblitz' ring flash.

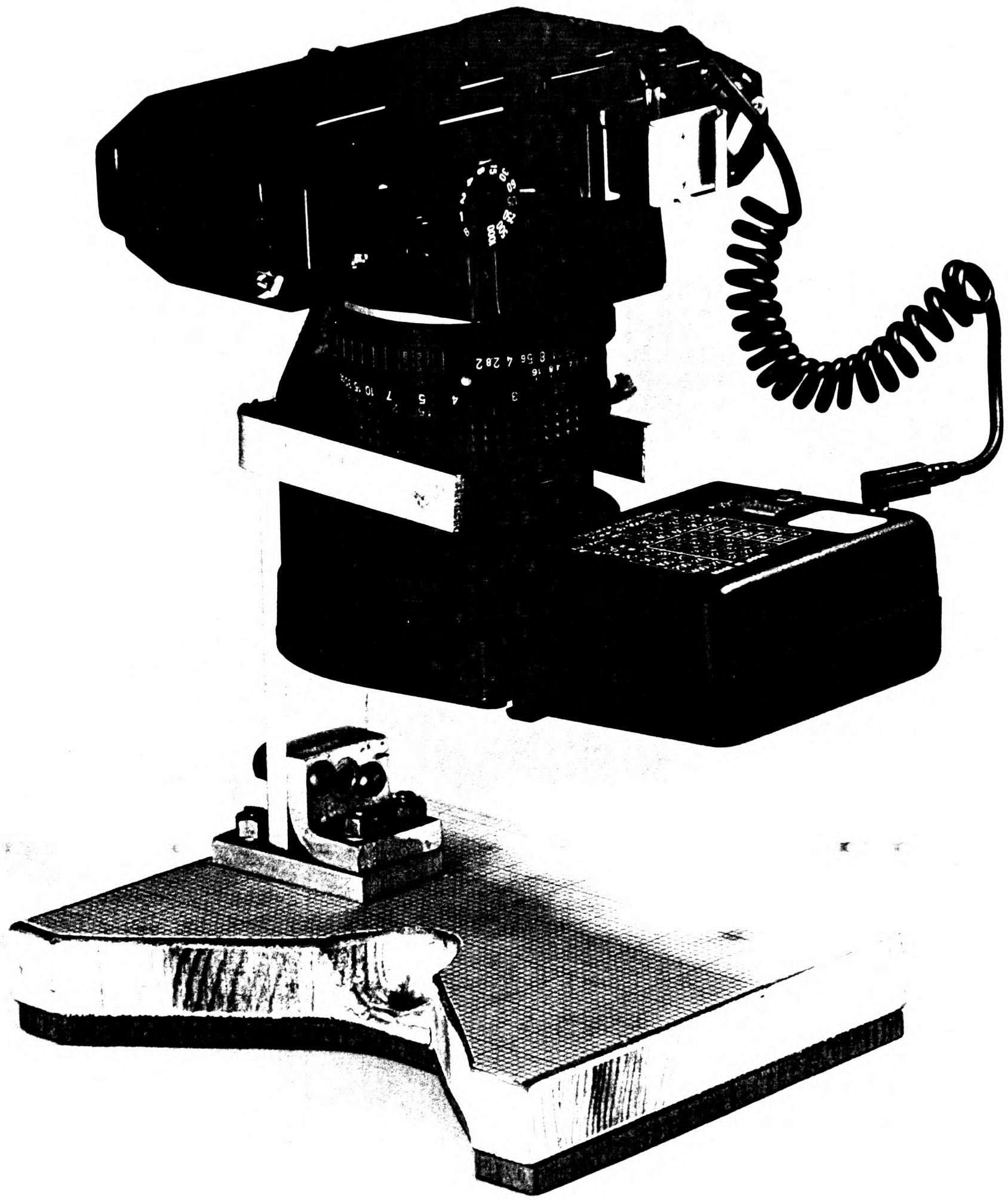
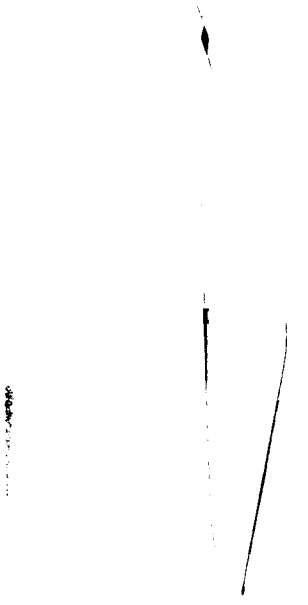


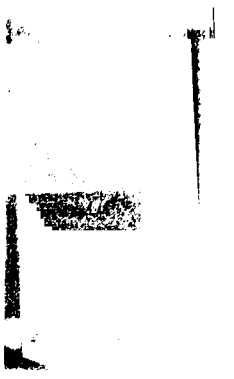
Plate 2. Standards taken as 0 and 2 in the analysis of culmen abrasion.

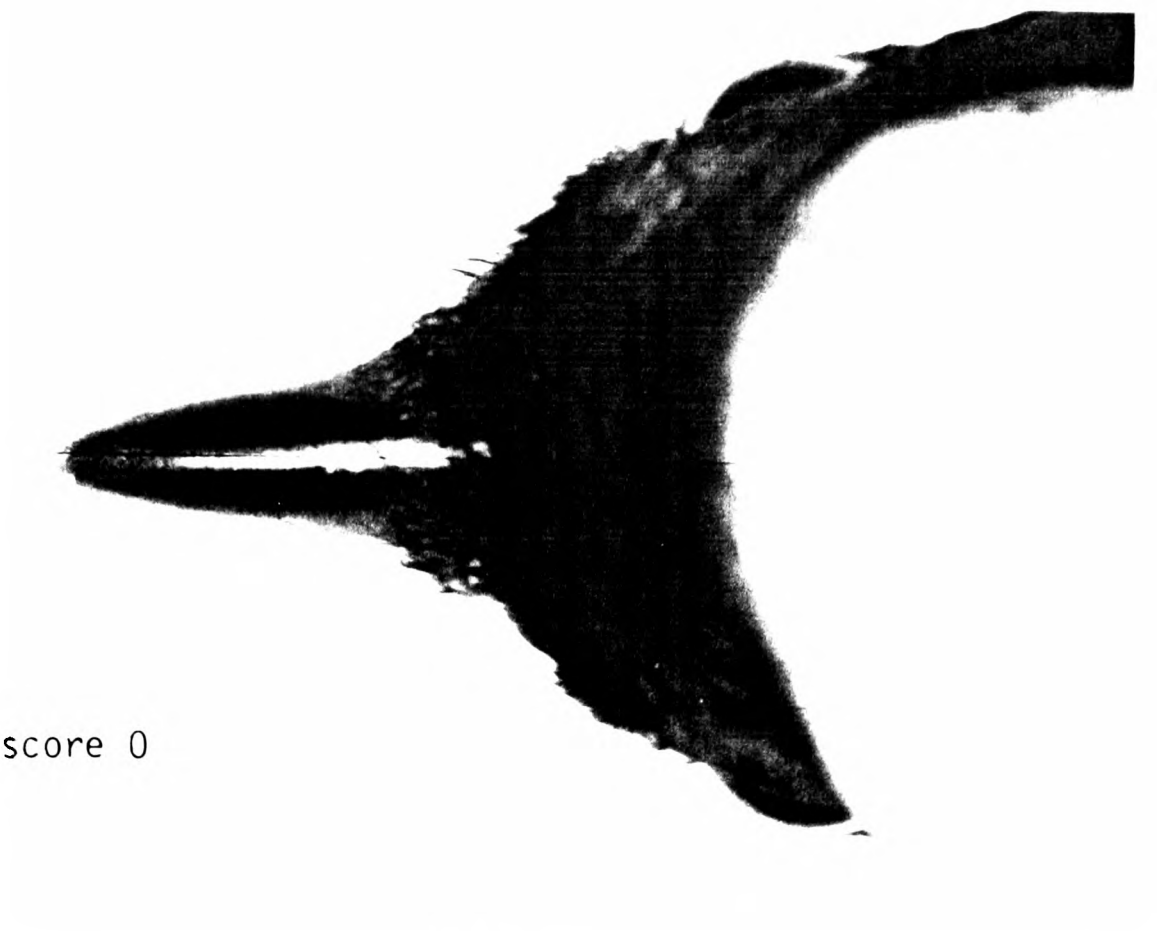
SCORE 0



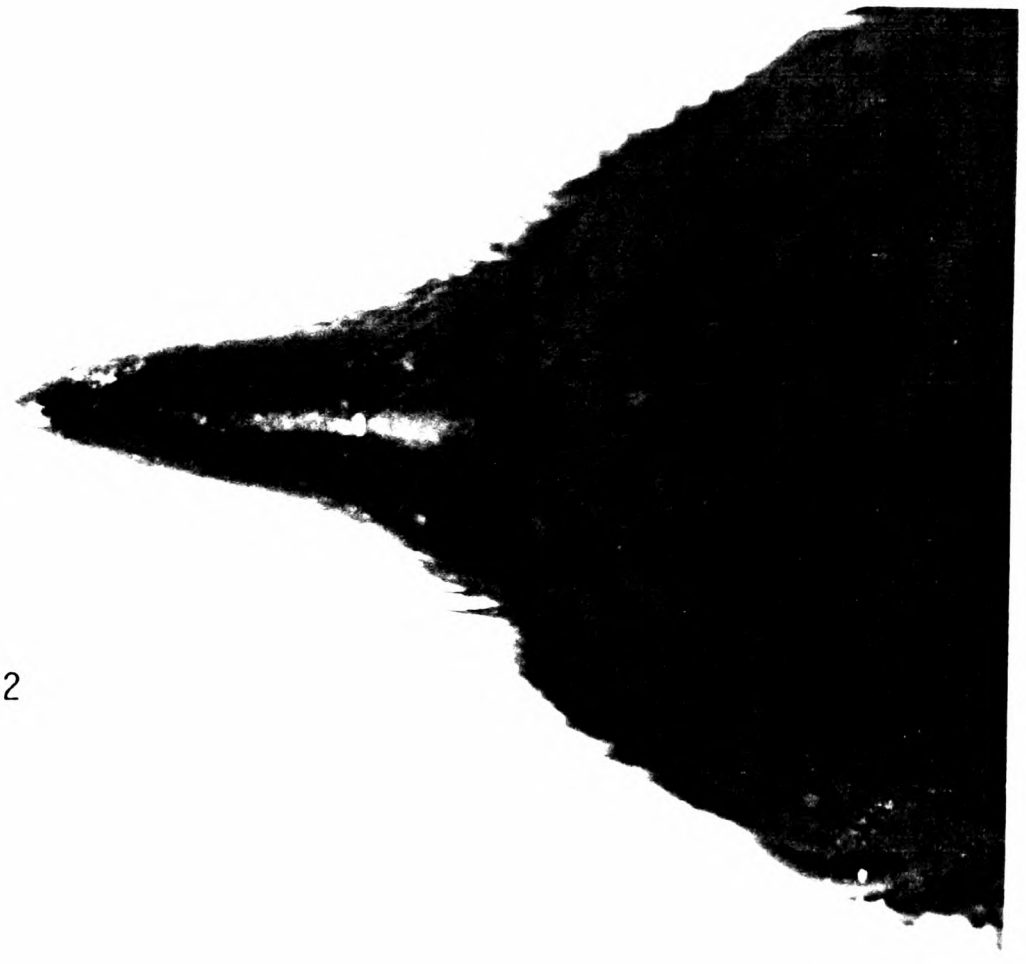
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SCORE 2





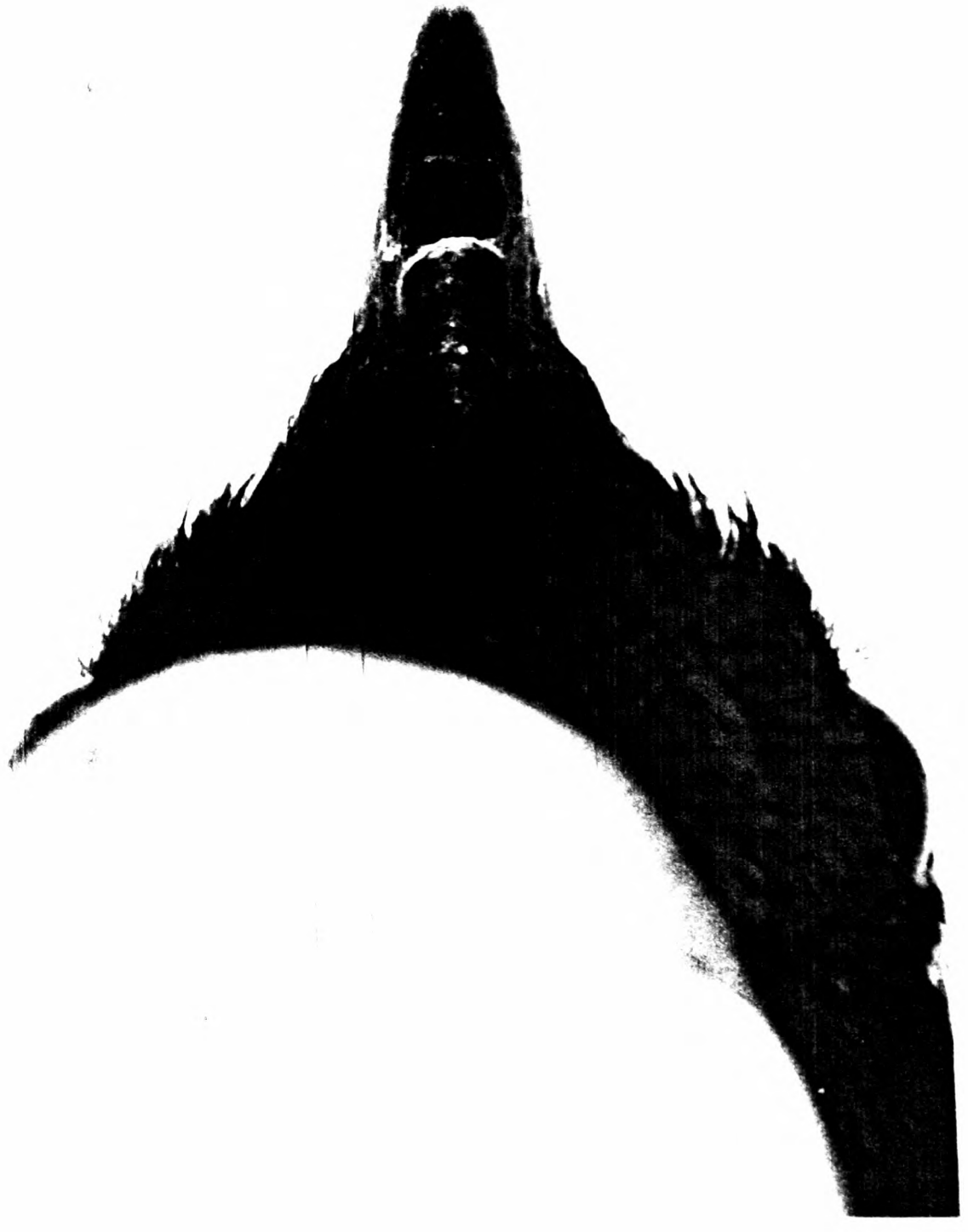
score 0



score 2

Plate 3. Lateral and dorsal exposures of bill moult in a male Great tit in spring 1984. The plate shows a clear step in the culmen, ahead of which (distally), moult is occurring.





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Appendices

Appendix 1.

Appendix 1. The total numbers of birds of each age and sex category handled in each month of the study. The table gives the total number of handlings. In summer, this is synonymous with the number of individuals. In winter it includes retraps. The number of individuals in these seasons are given in chapter 2.

Table A1.1

1982

	Jan	Feb	Mar	May	June	July	Oct	Nov	Dec
Adult male				28	6	Ø	8	4	Ø
1 Yr male				26	11	1	33	12	Ø
Adult fem.				23	4	1	4	2	Ø
1 Yr fem.				25	14	Ø	27	17	Ø
Total:				1Ø2	35	2	72	35	Ø

1983

	Jan	Feb	Mar	May	June	July	Oct	Nov	Dec
Adult male	9	16	7	31	8	Ø	17	43	4
1 Yr male	2Ø	29	9	53	2Ø	Ø	7	27	9
Adult fem.	6	1Ø	3	27	9	1	9	26	11
1 Yr fem.	23	16	6	64	26	Ø	4	1Ø	4
Total:	58	71	25	175	63	1	37	1Ø6	28

1984

	Jan	Feb	Mar	May	June	July	Oct	Nov	Dec
Adult male	4	15	18	7	28	Ø	14	1Ø	18
1 Yr male	6	3	15	9	38	Ø	27	39	36
Adult fem.	5	14	1Ø	14	25	1	9	9	11
1 Yr fem.	1	2	14	5	47	Ø	38	47	38
Total:	16	34	57	35	138	1	88	1Ø5	1Ø3

1985

	Jan	Feb	Mar	May	June	Absolute totals.
Adult male	9	7	9	35	5	36Ø
1 Yr male	18	1Ø	4	14	9	485
Adult fem.	8	2	11	3Ø	6	291
1 Yr fem.	18	14	6	21	8	495
Total:	53	33	3Ø	1ØØ	28	1631

A Note on the Independance of Data.

Many of the analyses carried out in this study involved large numbers of measurements of birds. Comparisons were then carried out between groups (eg: age, sex etc) of these measurements within seasons. In order to ensure that the results of these analyses were not weighted in any way by the inclusion of multiple measurements of the same individual, each bird was represented once only as described in chapter 2. This procedure was time consuming as data from all handlings were originally stored on the computer as a single database. However, as long as the probability of recapture is not correlated with some aspect of the character being investigated (eg: if for example only long-billed individuals were retrapped, so that the mean would be biassed upwards by the inclusion of retrap data) this safeguard is probably un-necessary in most cases if sufficiently large numbers of individuals were sampled. This is because as the sample size increases, the probability is reduced that any individual will have a significant effect on the mean. This is demonstrated for the present study by Table A1.2.

Table A1.2. This shows the mean, standard deviations, and sample sizes, of bill index of birds in each age and sex class in each season. In each case, the values are give for the whole data set which includes all handlings, and means derived from single handlings (measurements taken on the the first capture of the individual). Hence in the latter case, the sample sizes give the actual numbers of individuals sampled in each season. **Note: in no case did the two means or standard deviations differ significantly**

Autumn 1982

	All handlings		First captures	
Adult male	Ø.33525 + Ø.Ø1342	12	Ø.33518 + Ø.Ø14Ø8	11
lY male	Ø.32977 + Ø.Ø1483	44	Ø.33Ø29 + Ø.Ø1521	42
Adult fem.	Ø.3Ø183 + Ø.Ø1199	6	Ø.3Ø183 + Ø.Ø1199	6
lY fem.	Ø.311ØØ + Ø.Ø21Ø4	44	Ø.31175 + Ø.Ø2Ø74	43

Spring 1983

	All handlings		First captures	
Adult male	Ø.34872 + Ø.Ø1251	32	Ø.3468Ø + Ø.Ø12Ø7	2Ø
lY male	Ø.34465 + Ø.Ø1292	57	Ø.3462Ø + Ø.Ø1377	4Ø
Adult fem.	Ø.32721 + Ø.Ø1Ø39	19	Ø.3265Ø + Ø.Ø1249	12
lY fem.	Ø.32975 + Ø.Ø1221	44	Ø.31ØØ + Ø.Ø125Ø	36

Autumn 1983

	All handlings		First captures	
Adult male	Ø.3547Ø + Ø.Ø1156	64	Ø.35718 + Ø.Ø1142	38
lY male	Ø.34776 + Ø.Ø1171	42	Ø.34779 + Ø.Ø137Ø	24
Adult fem.	Ø.34Ø5Ø + Ø.Ø1122	46	Ø.34Ø77 + Ø.Ø1118	35
lY fem.	Ø.33888 + Ø.Ø1374	17	Ø.3357Ø + Ø.Ø1362	1Ø

Table A1.2 continued.

	All handlings		First captures	
Spring 1984				
Adult male	Ø.36ØØ9 + Ø.Ø1354	35	Ø.36Ø5Ø + Ø.Ø143Ø	2Ø
1Y male	Ø.34859 + Ø.Ø1919	22	Ø.34685 + Ø.Ø1922	2Ø
Adult fem.	Ø.35472 + Ø.Ø1574	29	Ø.35Ø33 + Ø.Ø1386	18
1Y fem.	Ø.34382 + Ø.Ø1162	17	Ø.34142 + Ø.Ø128Ø	12
Autumn 1984				
Adult male	Ø.3549Ø + Ø.Ø1314	42	Ø.35376 + Ø.Ø134Ø	37
1Y male	Ø.351Ø9 + Ø.Ø154Ø	1Ø2	Ø.351Ø6 + Ø.Ø1541	82
Adult fem.	Ø.3331Ø + Ø.Ø1246	29	Ø.33452 + Ø.Ø1242	25
1Y fem.	Ø.33624 + Ø.Ø1286	123	Ø.33612 + Ø.Ø1288	1ØØ
Spring 1985				
Adult male	Ø.35276 + Ø.Ø1Ø9	25	Ø.35244 + Ø.Ø1123	18
1Y male	Ø.34413 + Ø.Ø1122	32	Ø.3445Ø + Ø.Ø1131	28
Adult fem.	Ø.32981 + Ø.Ø113Ø	21	Ø.33127 + Ø.Ø1258	15
1Y fem.	Ø.33458 + Ø.Ø1495	38	Ø.33381 + Ø.Ø1416	36

Appendix 2.

Table A2.1. Correlation matrix showing product moment correlation coefficients among skeletal measurements of 20 complete specimens of **P. major newtoni**. Note, in 4 specimens, the rhamphotheca could not be removed, so that for correlations involving bill length and depth measurements, the sample size was 16. The characters measured were Ble Bill length, Bde Bill depth, Tib Tibiotarsus, Cwi Cranium width, Cht Cranium height, Jug Jugal bar, Bln Bill length measured from the tip to the distal edge of the nare, Tar Tarso-metatarsus length, Ste Sternum length, Hle Maximum cranial length (including bill), Sex as male = 1, female = 0.
Note: correlation coefficients in heavy type are significant (at least at P<0.05).

	Ble	Bde	Tib	Cwi	Cht	Jug	Bln	Tar	ste	Hle
Bd	**0.905**									
Tib	0.475	0.397								
Cwi	**0.499**	0.382	**0.477**							
Cht	0.286	0.276	**0.465**	**0.662**						
Jug	**0.806**	**0.612**	0.297	**0.663**	0.324					
Bln	**0.943**	**0.908**	0.448	0.398	0.186	**0.672**				
Tar	**0.518**	0.417	**0.474**	**0.825**	**0.567**	**0.707**	0.430			
ste	0.134	0.040	0.201	**0.526**	0.420	0.438	0.021	**0.653**		
Hle	**0.960**	**0.927**	0.484	**0.503**	0.313	**0.757**	**0.937**	**0.524**	0.115	
Sex	-0.024	0.000	0.216	**0.511**	**0.503**	**0.**183	-0.183	0.425	0.203	-0.028

Table A2.2 The correlation between bill characters and body size (represented by the cube-root of body weight). The analyses were carried out on resident (Wytham hatched) birds only. Significant values are given in bold type. Bill le. - Bill length, Bill de. - Bill depth, Bill in. - Bill, index. The right hand column gives the correlation between bill length and depth. Note: for autumn and spring seasons, the table states whether the birds were caught whilst feeding on beechmast - ON MAST or not - OFF MAST.

(A) Autumn / Spring

	Bill le.	Bill de.	Bill in.	n	Bill le/Bill de.
Autumn 1982 OFF MAST					
Adult male	Ø.58Ø	Ø.772	Ø.8ØØ	5	**Ø.882**
1Yr. male	**Ø.399**	Ø.281	-Ø.Ø73	34	**Ø.394**
Adult fem.	-	-	-	2	-
1Yr. fem.	**Ø.444**	Ø.316	-Ø.Ø61	25	Ø.Ø5Ø
Spring 1983 ON MAST					
Adult male	-Ø.Ø86	Ø.119	Ø.164	26	Ø.274
1Yr. male	**Ø.39Ø**	**Ø.658**	**Ø.397**	47	Ø.257
Adult fem.	Ø.355	Ø.216	Ø.136	8	Ø.586
1Yr. fem.	Ø.357	**Ø.582**	Ø.Ø98	24	Ø.245
Autumn 1983 ON MAST					
Adult male	**Ø.362**	Ø.Ø96	-Ø.222	53	Ø.118
1Yr. male	Ø.311	**Ø.372**	Ø.ØØ6	33	Ø.21Ø
Adult fem.	Ø.Ø68	**Ø.516**	**Ø.4Ø8**	3Ø	Ø.235
1Yr. fem.	**-Ø.665**	Ø.134	Ø.528	11	-Ø.Ø52
Spring 1984 OFF MAST					
Adult male	**Ø.73Ø**	Ø.Ø5Ø	**-Ø.54Ø**	21	Ø.248
1Yr. male	Ø.361	Ø.196	-Ø.193	13	-Ø.2Ø7
Adult fem.	Ø.Ø86	Ø.382	Ø.258	16	-Ø.ØØ26
1Yr. fem.	Ø.129	-Ø.3ØØ	-Ø.365	9	Ø.242

Table A2.2 cont[d].

Autumn 1984 ON MAST

	Bill le.	Bill de.	Bill in.	n	Bill le/Bill de.
Adult male	**Ø.447**	**Ø.597**	Ø.168	24	**Ø.428**
1Yr. male	Ø.139	**Ø.53Ø**	**Ø.37Ø**	71	Ø.Ø76
Adult fem.	Ø.428	**Ø.646**	Ø.267	17	Ø.261
1Yr. fem.	**Ø.321**	**Ø.578**	Ø.22Ø	58	**Ø.337**

Spring 1985 OFF MAST

	Bill le.	Bill de.	Bill in.	n	Bill le/Bill de.
Adult male	-Ø.334	Ø.197	Ø.488	13	Ø.391
1Yr. male	Ø.129	Ø.Ø77	-Ø.Ø27	21	Ø.Ø24
Adult fem.	Ø.317	-Ø.156	-Ø.296	8	-Ø.148
1Yr. fem.	**Ø.627**	Ø.Ø83	-Ø.312	15	Ø.Ø33

(B) Summer

Summer 1982

	Bill le.	Bill de.	Bill in.	n	Bill le/Bill de.
Adult male	Ø.195	Ø.Ø81	-Ø.143	34	Ø.123
1Yr. male	-Ø.Ø41	Ø.16Ø	Ø.156	36	Ø.Ø29
Adult fem.	-Ø.111	Ø.Ø42	Ø.1Ø5	25	Ø.213
1Yr. fem.	-Ø.Ø91	Ø.122	Ø.16Ø	36	Ø.113

Summer 1983

	Bill le.	Bill de.	Bill in.	n	Bill le/Bill de.
Adult male	Ø.Ø54	**Ø.315**	Ø.283	39	**Ø.34Ø**
1Yr. male	Ø.13Ø	**Ø.337**	Ø.163	72	Ø.1Ø3
Adult fem.	Ø.25Ø	Ø.Ø17	-Ø.22Ø	35	**Ø.359**
1Yr. fem.	Ø.2Ø2	Ø.Ø83	-Ø.Ø97	89	**Ø.438**

Summer 1984

	Bill le.	Bill de.	Bill in.	n	Bill le/Bill de.
Adult male	**Ø.457**	**Ø.4Ø4**	-Ø.112	34	**Ø.567**
1Yr. male	Ø.271	**Ø.335**	Ø.Ø56	47	**Ø.4Ø7**
Adult fem.	Ø.112	**Ø.33Ø**	Ø.195	39	Ø.223
1Yr. fem.	Ø.218	Ø.Ø84	-Ø.15Ø	52	Ø.Ø35

Summer 1985

	Bill le.	Bill de.	Bill in.	n	Bill le/Bill de.
Adult male	Ø.241	Ø.237	Ø.Ø61	39	Ø.Ø57
1Yr. male	Ø.Ø16	Ø.229	Ø.195	23	Ø.218
Adult fem.	Ø.172	-Ø.Ø22	-Ø.135	36	-Ø.Ø77
1Yr. fem.	Ø.Ø47	Ø.265	Ø.269	29	**Ø.477**

Table A2.3. The number of immigrant and resident Great tits of each age and sex class that bred in each habitat type during the summers of 1982-1985. See chapter 6. **Chisquare** values are given (df 4 or 5) in **bold print**. None was significant, indicating that there was no tendency for the two groups to occupy habitats differentially.

First-year birds.

		Habitat types						
Summer 1982.		A	B	C	D	E	F	
Female	immigrants	8	5	3	1	2	1	
	residents	5	2	8	Ø	1	2	**5.828** ns
Male	immigrants	2	2	3	1	5	1	
	residents	9	5	6	Ø	2	1	**7.267** ns
Summer 1983.		A	B	C	D	E	F	
Female	immigrants	6	5	14	1	9	1	
	residents	11	8	2Ø	4	9	2	**1.828** ns
Male	immigrants	3	2	8	Ø	3	2	
	residents	13	11	16	6	8	1	**6.729** ns
Summer 1984.		A	B	C	D	E	F	
Female	immigrants	6	2	5	3	2	Ø	
	residents	2	6	7	8	8	3	**9.149** ns
Male	immigrants	2	2	2	2	1	3	
	residents	8	7	9	4	7	Ø	**1Ø.182** ns
Summer 1985.		A	B	C	D	E	F	
Female	immigrants	2	3	2	1	6	Ø	
	residents	2	3	8	1	1	Ø	**7.145** ns
Male	immigrants	4	1	2	1	3	Ø	
	residents	1	2	7	Ø	2	Ø	**6.Ø79** ns

Table A2.3 contd.

Adult birds.

Summer 1982.		A	B	C	D	E	F	
Female	immigrants	Ø	1	2	1	3	Ø	
	residents	3	2	1Ø	4	1	Ø	**6.779** ns
Male	immigrants	1	1	7	4	3	Ø	
	residents	3	2	7	2	2	1	**3.173** ns

Summer 1983.		A	B	C	D	E	F	
Female	immigrants	2	6	4	1	1	1	
	residents	2	6	7	3	2	1	**1.184** ns
Male	immigrants	2	7	5	2	4	Ø	
	residents	3	6	7	Ø	1	2	**6.389** ns

Summer 1984.		A	B	C	D	E	F	
Female	immigrants	4	1	6	Ø	4	1	
	residents	3	6	3	4	6	1	**8.119** ns
Male	immigrants	Ø	1	4	2	3	1	
	residents	4	3	6	5	5	1	**2.734** ns

Summer 1985.		A	B	C	D	E	F	
Female	immigrants	4	1	6	Ø	3	Ø	
	residents	1	6	9	2	3	1	**7.567** ns
Male	immigrants	2	3	7	Ø	2	2	
	residents	2	7	7	4	4	Ø	**6.944** ns

Table A2.3 contd.

All years combined (to increase sample sizes).
(All Chi-square have 5 d.f)

All First-years		Habitat types A	B	C	D	E	F	
Female	immigrants	22	15	24	6	19	2	
	residents	20	19	43	13	19	7	6.256 ns
Male	immigrants	11	7	15	4	12	6	
	residents	31	25	38	10	19	2	10.085 ns

All adults		Habitat types A	B	C	D	E	F	
Female	immigrants	10	9	18	2	11	2	
	residents	9	20	29	13	12	3	7.168 ns
Male	immigrants	5	12	23	8	12	3	
	residents	12	18	27	11	12	4	2.061 ns

Appendix 3. Observations on diurnal fattening in the Great tit.

Appendix 3. Observations on diurnal fattening in the Great tit.

It has long been known that body weight changes markedly during the day in the Great tit. Owen (1954) showed that body weight increased by 5-10% during the day in winter and that this weight was lost overnight. He further showed that weight correlated negatively with mean daily temperature. These relationships have now been shown in several Great tit populations, and Van Balen (1967) showed that this weight change was largely due to circadian changes in the amount of fat stored in discrete fat bodies or depots. Haftorn (1976) showed that the rate at which fattening occurred with declining temperature, increased with latitude. That is, at high latitudes, the regression of fat on temperature was steeper than at lower latitudes. Changes in fat depots have been reported for several species. General accounts of the occurrence and physiology of fat depots in passerines were given by King (1970) and Blem (1976). Blem (1976) points out that avian fat depots are not involved in fat synthesis, but only in its storage. Further, that the increase in fat stored in adipocytes occurs without a corresponding change in either the fat-free dry weight or the relative water content of the body. Valyathan & George (1969) showed that depot fat took priority as an immediate energy source and that intra-cellular muscle lipid was not used until the depot fat had been exhausted. Depot fat is drawn upon directly during the day and in winter is particularly important as an energy source at night (King 1970, Blem 1976). The scoring of depot fat gives a reliable estimate of the relative amount of fat on the whole body (Blem 1976).

Prys-Jones (1977) studied fat deposition in wintering Reed Buntings Emberiza schoeniclus and Yellowhammers E. citrinella. He found that the best predictor of total fat content (explaining 46% of the variance) was the

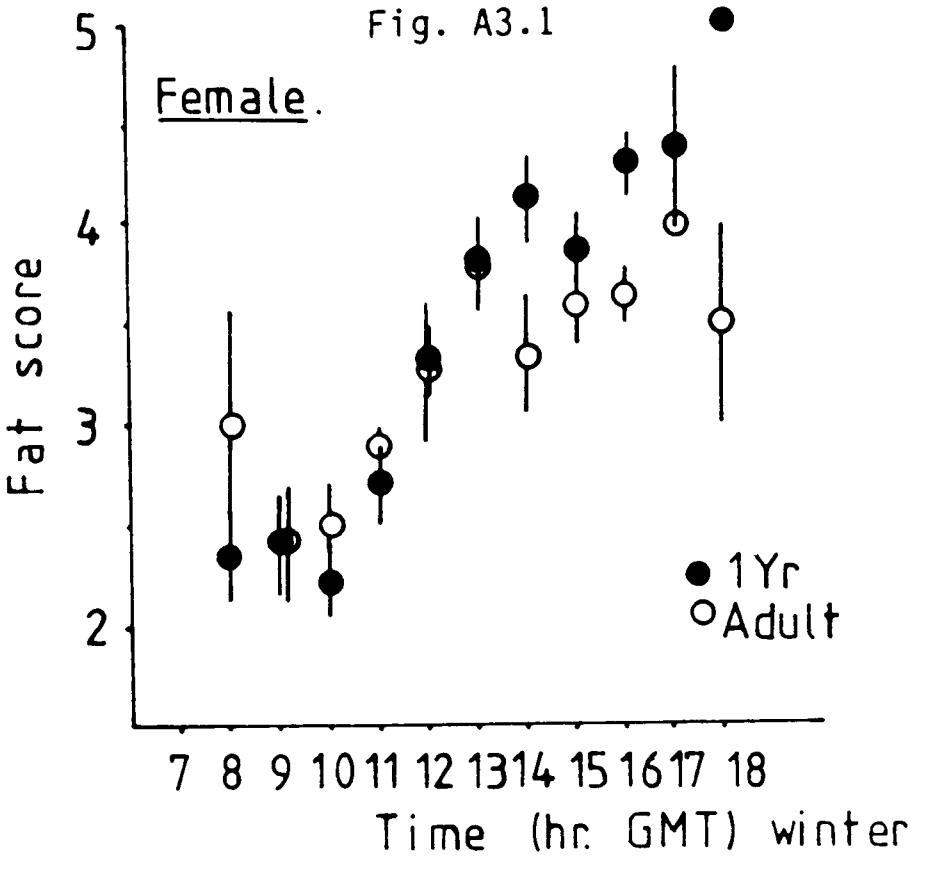
twenty-year mean of daily temperature. Temperature on the day of collection had little effect on the total fat. In the Yellowhammer, body size also explained a significant part of the variation, but this was only 8%. This was not found in the Reed Bunting. He suggested that in species with a predictable food supply, fat storage might be determined intrinsically by the length of night-time in prospect. In the Great tit, food supply is rarely this predictable and fat score is correlated highly with the temperature on the day of capture. Table A3.1 gives partialised r^2 values for fat score with time and temperature in each age and sex class for all birds handled in winter at 'unmanipulated' feeding sites (see next section). In both sexes, fat scores were less influenced by temperature in adults than in first-year birds.

To test whether the birds fattened in response to day length, a stepwise multiple regression was carried out with fat as the criterion variable and time, daylength and mean temperature on the day of capture as predictors. Analyses were carried out on the sexes separately. When this was done, r^2 values for time and temperature were essentially as given in table A3.1. Daylength explained a further 2.0% of variance in males and 1.68% in females. Neither of these results were significant, indicating that, unlike the Buntings described earlier, Great tits responded to immediate conditions.

Figures A3.1 and A3.2 show the relationship between fat score and time of day in each age and sex class at sites used in Table A3.1. The increase in fat through the day shows a more or less sigmoidal pattern with a maximum slope around mid-day.

The use of fat score as an indicator of individual condition has the advantage over body weight that it varies independently of body size whilst body weight must include a size component. However, any covariance between body size and fat score within an age/sex class, suggests the influence of

Fig. A3.1 Changes in fat levels through the day in female Great tits. The graph shows the Mean + 1se of fat score for all females trapped in winter at unpredictably baited sites in Wytham.



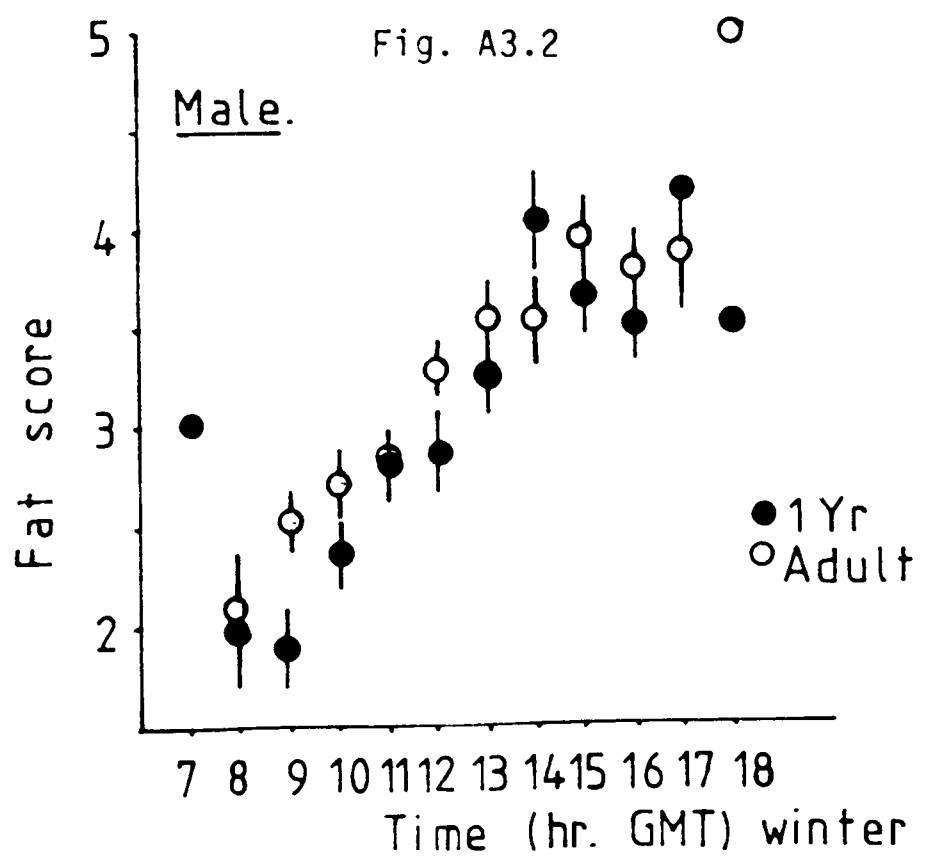


Fig. A3.2 Changes in fat levels through the day in male Great tits. The graph shows the mean + 1se of fat score for all males trapped in winter at unpredictably baited sites in Wytham.

social interaction which is mediated by body size (Garnett 1976, Drent 1981). Table A3.2 shows the variance in winter body weight explained by time of day and temperature for the same statistical populations used in Table A3.1. In comparing Tables A3.1 and A3.2, note that considerably more of the variance in fat score than body weight was explained by these two variables.

Fat scores of zero and five theoretically include a slightly greater range of body weight than do the other classes, as they include starving and obese birds respectively. However, in practice, this has very little influence as very few birds fell into these categories as shown in Table A3.3. Figure A3.5 shows the relationship between fat score and body weight in all winter trapped birds. The sexes are shown separately. The difference in intercept between sexes is due to the difference in body size. The relationship was linear and the sexes were essentially the same in slope. Hence fat scores are comparable between sexes.

Figures A3.3 and A3.4 show the relationships between fat score and temperature in each age and sex class. In both sexes, the slope was higher for first-year than adult birds. In males this was significant ($t = 2.25$, $P < 0.05$ in comparison of Z-transformed correlation coefficients).

Palokaugar & Vihko (1972) found that the depot fat of Great tits contained significantly more saturated fatty acids in summer than in winter. They suggested that this would allow fat to be liberated more easily in winter than summer. Figures A3.6 and A3.7 show that the pattern of daily fattening was the same in summer as in winter although in summer fat scores were lower at the end of the day. Table A3.4 shows the variance in fat score and body weight explained by time of day. As in winter, considerably more variance in fat score than body weight is explained. Fat score and body weight were themselves very poorly correlated.

Figure A3.3. The relationship between fat scores and mean daily temperature in female Great tits in winter (all years combined). The equations for the regression lines are 1Yr: Y=3.72-0.0963X, Adult: Y=3.39-0.0628X. These were statistically significant - see text.

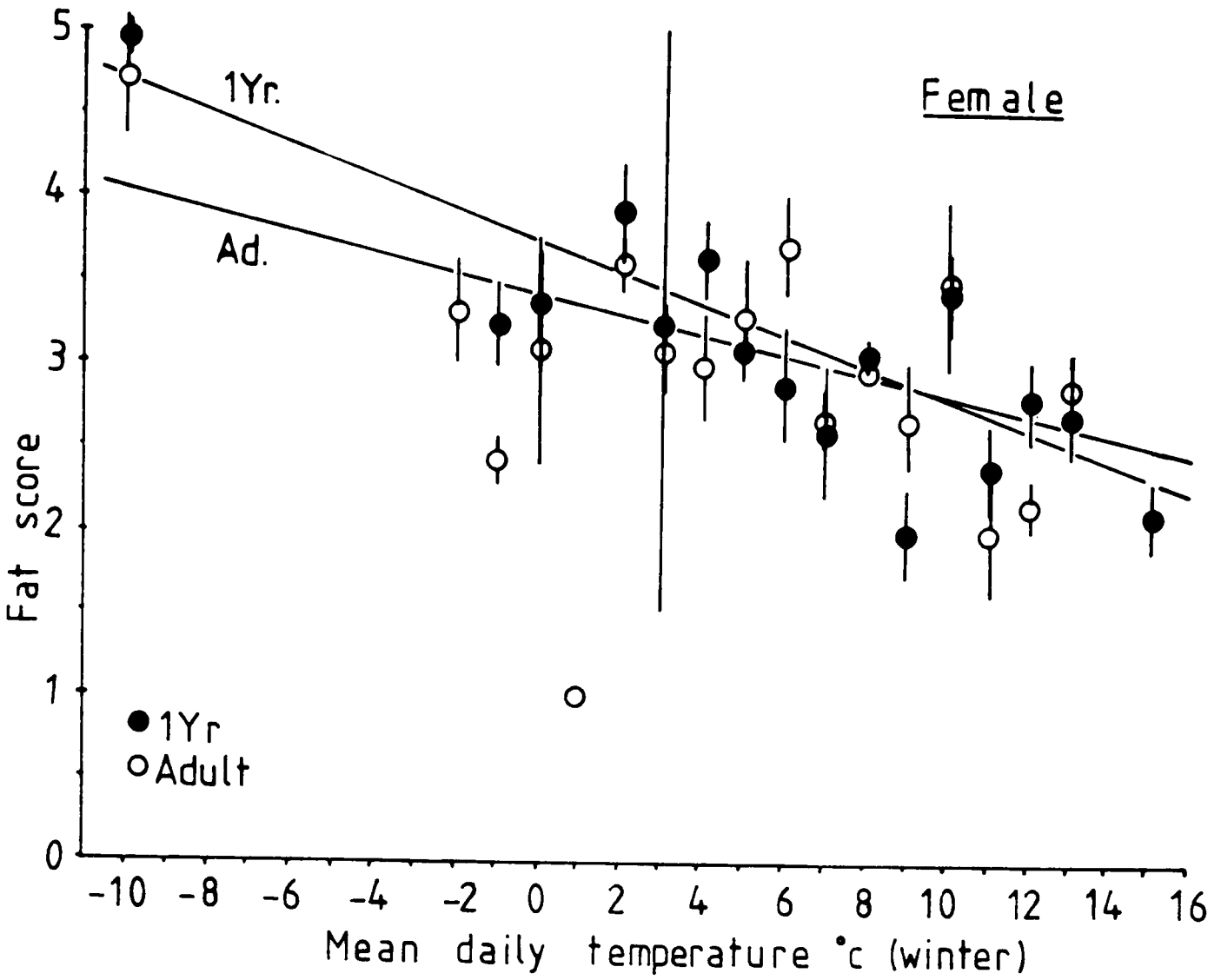


Figure A3.4. The relationship between fat scores and mean daily temperature in male Great tits in winter (all years combined). The equations for the regression lines are 1Yr: Y=3.42-0.0996X, Adult: Y=3.40-0.0544X. These were statistically significant - see text.

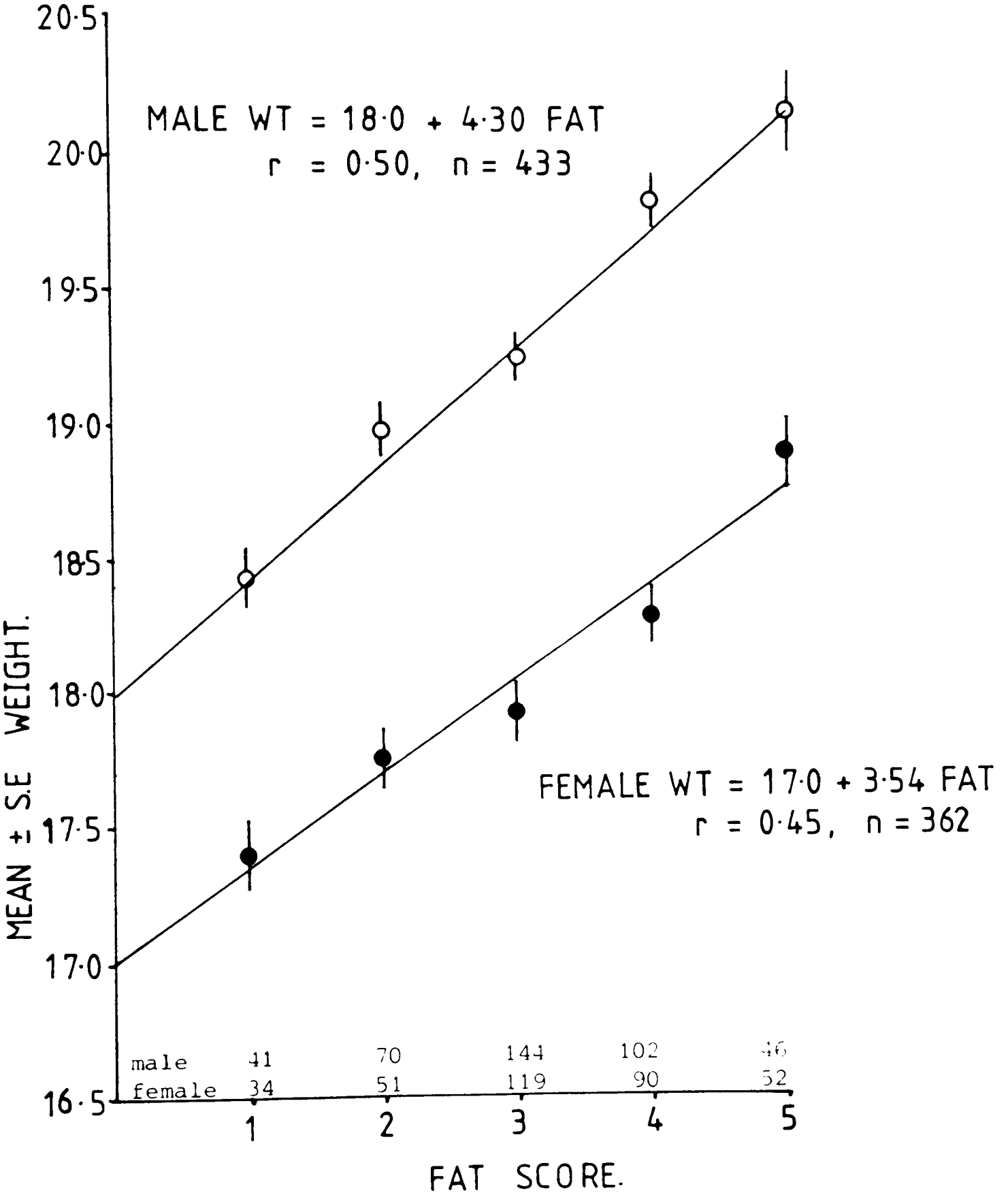


Figure A3.5 The relationship between fat score and body weight in the Great tit. The open circles show males, the closed circles show females. Sample sizes are given along the x axis. The Difference in the intercepts of the regression lines is due to the sex-difference in body size.

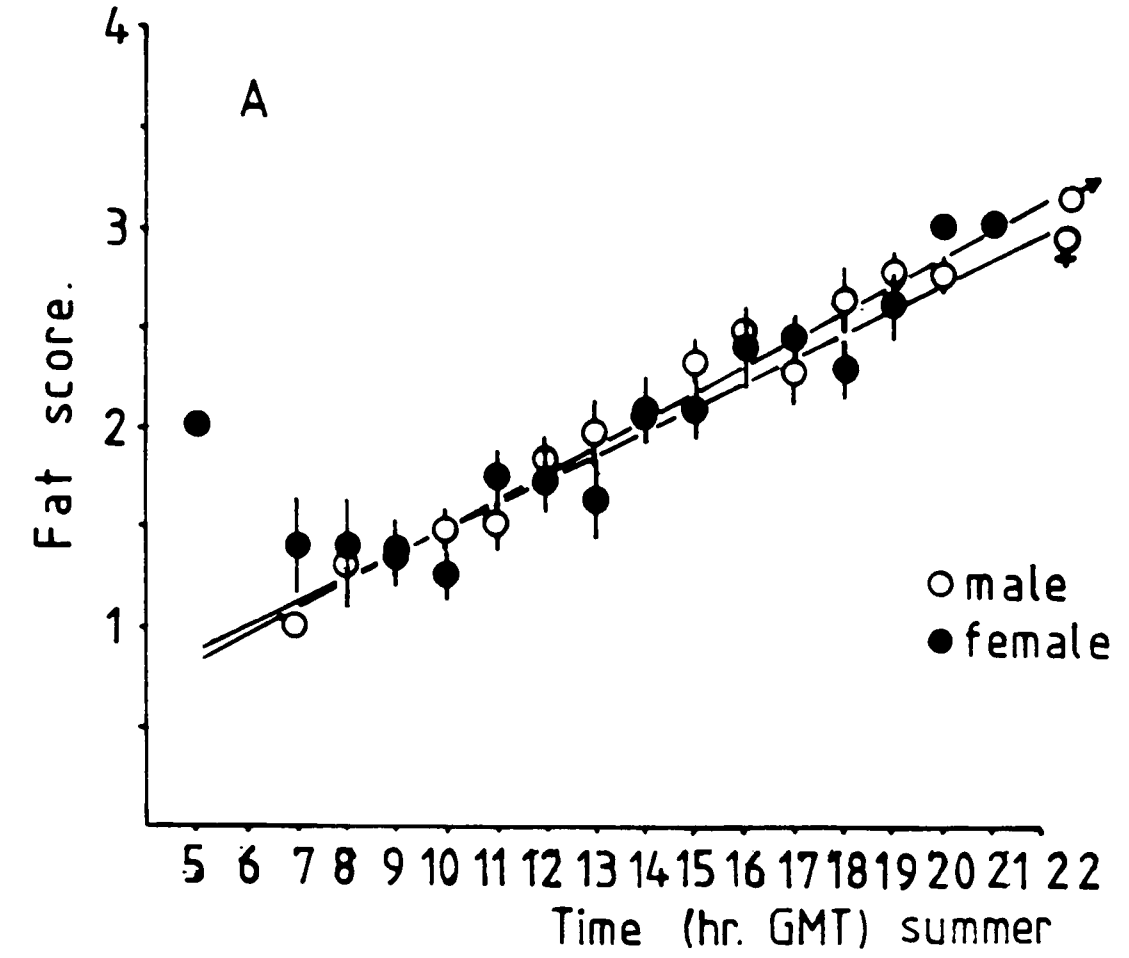


Figure A3.6. The relationship between fat scores and time of day in male and female Great tits in summer (May and June - all years combined). The regression equations are: Male: Y=Ø.166+Ø.134X, Female: Y=Ø.291+Ø.122X. These were statistically significant - see text.

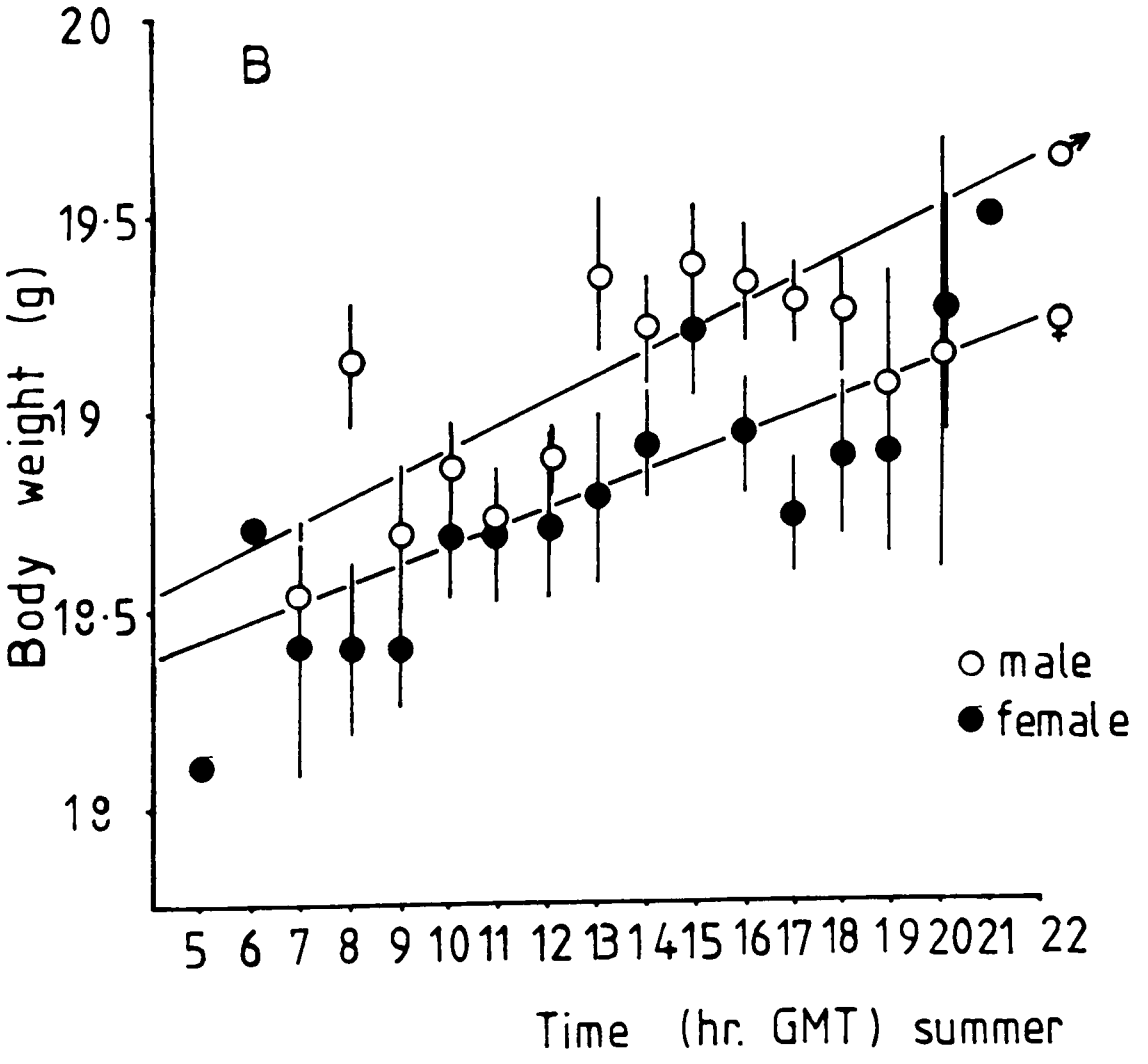


Figure A3.7. The relationship between body weight and time of day in male and female Great tits in summer (May and June - all years combined). The regression equations are: Male: Y=18.3+Ø.Ø617X, Female: Y=18.2+Ø.Ø457X. These were statistically significant - see text.

Table A3.1 The percentage of variation in fat score explained by time of day and temperature in the Great tit. Data were analysed within age and sex classes and only captures from unmanipulated sites have been used.

Age/sex.	n.	Time[+]		Temperature[*]		Total
Ad male	197	29.11%	P<Ø.ØØ1	5.45%	P<Ø.Ø5	34.56%
1Y male	291	24.96%	P<Ø.ØØ1	12.58%	P<Ø.ØØ1	37.54%
Ad female	14Ø	16.53%	P<Ø.ØØ1	4.53%	P<Ø.Ø5	21.Ø6%
1Y female	214	33.97%	P<Ø.ØØ1	7.95%	P<Ø.Ø1	41.92%
All	842	24.33%	P<Ø.ØØ1	11.41%	P<Ø.Ø1	35.74%

+ All time correlations were positive. * All temperature correlations were negative.

Table A3.2 The percentage of variation in body weight explained by time of day and temperature in the Great tit. Data were analysed within age and sex classes and only data from unmanipulated sites have been used. Compare with Table A3.1.

Age/sex.	n.	Time+	Temperature*	Total	r^2fat
Ad male	197	9.57% P<Ø.Ø1	Ø.54% NS	1Ø.11%	33.5%
1Y male	291	4.8Ø% P<Ø.Ø5	1.87% NS	6.67%	23.4%
Ad female	14Ø	7.99% P<Ø.Ø1	Ø.54% NS	8.53%	22.4%
1Y female	214	3.45% P<Ø.Ø5	7.47% P<Ø.Ø1	1Ø.92%	18.9%

+ All time correlations positive. * All temperature correlations negative.

Table A3.3 Fat score distributions by age and sex class for all winter trapped Great tits at unmanipulated sites.

Fat Score	Ad Male	1Y Male	Ad Female	1Y Female	n.
Ø	Ø	Ø	Ø	Ø	Ø
1	11	3Ø	1Ø	24	75
2	31	39	2Ø	31	121
3	63	81	52	67	263
4	52	5Ø	34	56	192
5	2Ø	26	14	38	98
n	177	226	13Ø	216	749

Table A3.4 The percentage of variation in fat score and body weight explained by time of day in breeding Great tits. All correlation were positive.

Sex	Fat	P	n	Weight	P	n	r^2 fat & body weight.	
Male	31.5%	<Ø.ØØ1	255	6.9%	<Ø.Ø1	324	4.4%	P<Ø.Ø5
Female	22.7%	<Ø.ØØ1	278	2.6%	NS	347	5.5%	P<Ø.Ø5

A.3.1 Fat reserves as a measure of individual condition.

Pond (1981) has argued that despite the obvious benefits of fat storage, carrying fat itself imposes a cost in terms of higher flight costs and in the individual's ability to escape from predators. The likelihood of this will vary among species, but may be applicable to small passerines. Following this argument, one should expect birds to carry the minimum amount of fat required to sustain them through a period of fasting (such as at night).

To test the effect of food availability on fat storage, sampling was carried out at four sites during the winter 1983/84. Three different baiting regimes were used at these sites as described in Table A3.5. Only six birds (of 299 trapped) occurred at more than one of these sites during the period and these were all movements between Rough Common and Brogden's belt (3.8% of the combined catch at these two sites) so that the sites were effectively isolated.

Figure A3.8 shows the regression lines for fat score on time of day for all birds caught at each of these sites. At Brogden's Belt and Rough Common fat score increased significantly through the day. The regression slopes at these sites did not differ significantly. At Holywell Meadow and Marley Wood however, fat scores remained remarkably constant during the period of capture. There was no significant covariance between fat score and time of day at these sites, nor did the correlation coefficients differ significantly from each other. The difference between correlation coefficients for sites 1 and 2 combined versus sites 3 and 4 combined were highly significant ($t = 6.58$, $P<0.001$). This difference was also significant for data collected between 10.00 and 13.00 hours ($t = 2.817$, $P<0.01$). Two points may be made from these

Table A3.5 Food avaiability at four trapping sites during the winter of 1983/84.

(1) Brogden's Belt - No additional food was provided. Birds were trapped whilst feeding on mast between Ø8.ØØ and 17.ØØ hours. Trapping in Spring and Autumn, mostly Autumn 1983.

(2) Rough Common - Food was provided randomly in time though feeding was always within a 14 day period. The site was baited for one day before trapping and netting was from Ø8.ØØ till 17.ØØ hours. Trapping in Spring and Autumn

(3) Marley Wood, Wytham - Food was provided daily and in the morning throughout the trapping period. There was usually an abundance of food at the site. Trapping was between Ø9.ØØ and 15.ØØ hours at irregular intervals. Trapping in Autumn.

(4) Holywell Meadow, Oxford - As Marley but trapping was weekly. Work carried out by Holywell Ringing Group. Trapping in Autumn.

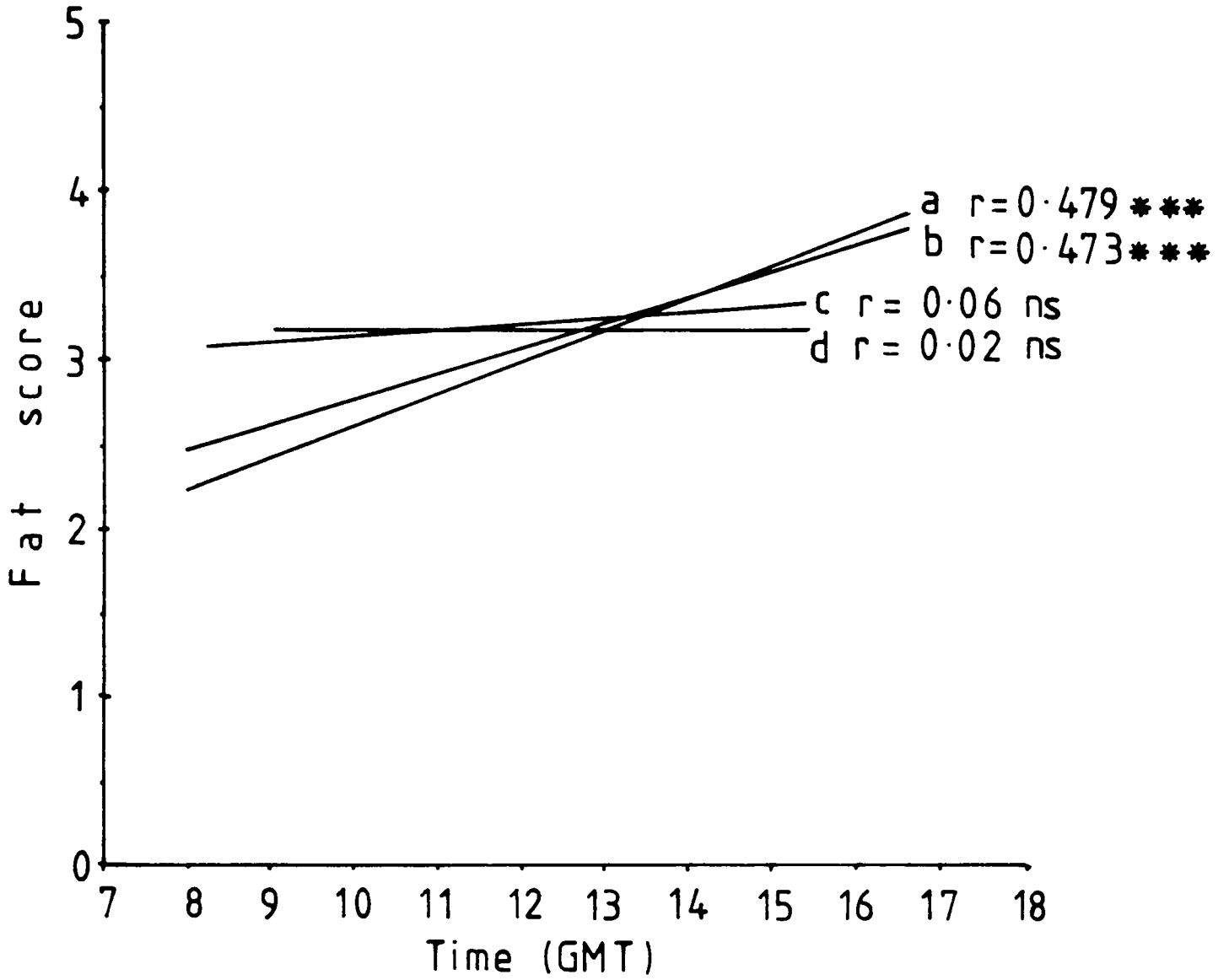


Figure A3.8. The relationship between fat scores and time of day at four feeding stations providing different feeding conditions. See text for details. Site (a) Brogden's Belt: Y=1.12+Ø.17X (F=14.12,P<Ø.ØØ1) and Site (b) Rough Common: Y=Ø.66+Ø.19X (F=3Ø.9,P<Ø.ØØ1) show foragers at beechmast and an unpredictably baited site. Site (c) Holywell Meadow: Y=2.75+Ø.Ø4X (F=Ø.339,P>Ø.1) and Site (d) Marley Wood: Y=3.12+Ø.ØlX (F=Ø.ØØ8,P>Ø.1) show foragers at predictably baited sites.

results. First, random provision of food as bait (as at Rough Common) had no effect on the rate of fattening, so that data collected in this way are comparable with birds caught at unbaited sites. Secondly, although the birds at Marley and Holywell meadow must have fattened rapidly in the morning or early evening so as to compensate for the overnight fat loss, they maintained a more constant fat level through the middle of the day, though this level was not on average lower than at unbaited sites. However, the experiment suggests that food availability influences the pattern of fattening through the day.

To examine the influence of dominance on fat storage, fat scores for birds trapped at the four sites were adjusted to 12.00 noon and $0^{o}C$ using regression equations calculated for each age and sex class at each site. Table A3.6 shows the mean $\pm$ sd of standardised fat scores form each age and sex class at each site. Data from Rough Common and Brogden's Belt have been pooled in Table A3.6, but data from Spring and Autumn trapping seasons are shown separately. The rank order of fat score is given. In every case, first-year females carried the most fat, and in three cases, this was significantly more than was carried by the class with the least fat. There is a tendency for the ranking for fat scores to correspond inversely with the ranking of the dominance hierarchy. This was best shown at the 'manipulated' sites.

When food was predictable and abundant, members of the most dominant class carried the least fat. Those of the least dominant class carried the most fat. This ranking was also observed at Rough Common during the Spring of 1983 when there was the greatest niche segregation between sexes (Table A3.7). Since fat level correlates negatively with temperature, being highest under the most severe conditions, there can be no doubt that dominant individuals were able to carry more fat than they did. That they often carried the least fat suggests that they were 'buffered' by the greater predictability and access

Table A3.6 Mean fat scores of four age/sex classes at baited and unbaited sites. Fat scores were adjusted to 12oo noon and Ø°c.

	Holywell Meadow	Marley Wood	Rough Common / Brogden's Belt Autumn	Spring
Ad. male	2.92±Ø.77 n=19 [1]	3.15±Ø.77 n=13 [1]	3.Ø4±Ø.74 n=55 [3]	3.4Ø±Ø.76 n=26 [2]
1Y. male	3.Ø3±Ø.91 n=36 [2]	3.46±Ø.62 n=12 [2]	2.78±Ø.74 n=39 [1]	3.47±Ø.69 n=17 [3]
Ad. fem.	3.11±Ø.79 n=11 [3]	n=7 [3.5]*	3.Ø1±Ø.81 n=45 [2]	2.95±Ø.77 n=25 [1]
1Y. fem.	3.24±1.1Ø n=34 [4]	4.23±Ø.46* n=4 [3.5]*	3.37±Ø.68 n=12 [4]	4.21±Ø.88 n=14 [4]
	t=NS	t=4.18,P<Ø.ØØ1	t=4.49,P<Ø.ØØ1	t=2.56,P<Ø.ØØ1

* Female age classes pooled to increase sample size.
t values given are tests between means of highest and lowest ranks.
Rankings are given in squared brackets.

Table A3.7 Standardised fat scores among age/sex classes of Great tits at Rough Common during the Spring of 1983.

Status	Mean±1sd fat score.
Ad. male	2.67±1.13 n=25 [1]
1Y. male	2.90±1.14 n=39 [2.5]
Ad. female	2.90+1.10 n=16 [2.5]
1Y. female	3.33±1.14 n=29 [4]
	t=2.05, P<0.01

to food that was gained from their status. This is supported by the greater rate of fattening with declining temperature observed in first-year birds, and also by De Laet (1985) who found that subdominant Great tits were the first to return to a feeder after a predator had passed. It also agrees with Pond's argument that carrying fat carries a cost, and that in buffering the dominant individual against its environment, high status allows it to carry less fat. These results imply that fat scores are not equally applicable across all age/sex classes as indicators of individual condition.

One further observation should be noted. Table A3.8 shows the mean fat scores carried by survivors and non-survivors in first-year males in each winter. Fat scores have been standardised for time and temperature by multiple regression. Note that in two winters first-year males that survived the winter (or at least established a territory within Wytham) carried significantly more fat than those that were not retrapped after the winter. No comparison was significant in any other status class. This suggests that at least in this group - attempting to establish a territory for the first time (which distinguishes it from all other classes) - carrying fat may be important.

Table A3.8 Standardised fat score for winter surviving and non-surviving (see chapter 7) first-year males.

Winter	survived	n.	not survived	n.	t
82/83	3.43±Ø.97	24	2.48±Ø.96	17	3.Ø7 **
83/84	4.66±Ø.35	3	2.9Ø±Ø.93	63	7.58 ***
84/85	2.52±Ø.91	7	2.81±Ø.98	127	NS.

Appendix 4.

The British Great tit differs from the continental bird on its smaller average size, and in having duller plumage although the colour pattern is the same. The black of the crown and the broad belly stripe is not as pure as in the continental bird and is almost without gloss. The cheeks are a dirtier white. The ash-grey of the rump is reduced to a minimum, being squeezed out by the olive-green of the back. The otherwise blueish ash-grey tail feather edges are - in the British bird - blackish, or at least much darker than in the central European specimens. The edges of the secondaries similarly show a marked suffusion with the back colour and the bar formed by the tips of the upper wing coverts is less clear and clean in colour. The yellow of the underside is less intense with a somewhat greenish flush.

L. Olph Galliard recognised this form as distinct from the European Great tit but gave no name. I make so bold as to name this insular subspecies after the greatly honoured master of scientific ornithology at Cambridge, Professor A. Newton.

J.P. Prazak, 1894.
(Translated by M.G. Wilson).

Appendix 4. Bill variation and the taxonomy of *Parus major newtoni*.

A4.1. Introduction.

The extract above is a translation of the full original description (type description) of the British Great tit, and the type specimen stated:

Typus: K.u.k. naturl. Hofmuseum in Wien. Nr. 10664, male.

is the type specimen for *Parus major newtoni*. The subspecific circumscription was based on an examination of nineteen British specimens at the Hofmuseum in Vienna. We are not told the sex ratio of this series, nor are we told the localities of collection of the *P. m. major* specimens with which they were compared. There is a hint that they are from central Europe, probably Austria, hence these are probably not neighbouring populations, but are widely separated along a cline of body size and colouration, and lying on different sides of the Alpine barrier (Harrison 1945, Snow 1953). Prazak (1894) lists a series of distinct characters. Few (if any) of these withstand closer scrutiny (Hartert 1907, Saunders 1920, Witherby *et al*. 1927, 1938-41), but two points are of interest. First, he includes no mention of the bill. Secondly, he states that the British bird is smaller.

The first clear mention of a racial difference in the bill comes from Hartert (1907) who reports of *P. m. newtoni*:

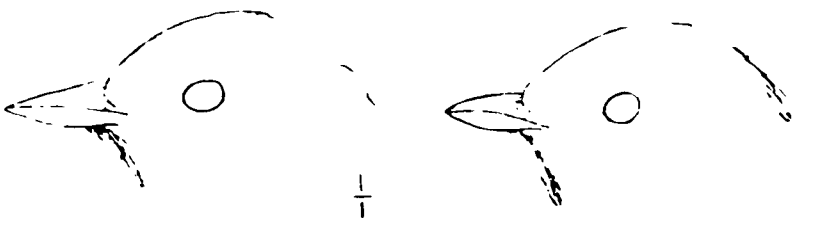
(it is...) "Easily distinguished from *Parus major major* (typical in Scandinavia, Germany, France, Holland, Belgium etc) by its stout, powerful bill. The alleged differences in colour are not constant."

E. Hartert (1907).

Figure A4.1

Parus major newtoni Prazak—THE BRITISH GREAT TITMOUSE.

PARUS MAJOR NEWTONI Prazak, Orn. Jahrb., v, p. 239 (1894 –England). *Parus major* Linnaeus, Yarrell, i, p. 479 ; Saunders, p. 103 ; *P. m. newtoni* Prazak, Hartert, Brit. B., i, p. 213.



The British Great Titmouse.
(*Parus m. newtoni*)
Note larger bill.

The Continental Great Titmouse.
(*Parus m. major*).
Note smaller bill.

Reproduced from Witherby et al. (1938-1941).

Between 1907 and 1945, no systematic analysis of bill differences was made. Hartert (1907) himself gave no quantitative evidence for his assertion. Saunders (1920) also reported that P. m. newtoni (hereon referred to as newtoni), differed only on the form of the bill, but again, gave no quantitative evidence. Witherby et al. (1927) illustrated the difference in bill form (reproduced in Figure A4.1) and stated that the bill of newtoni tended to be longer, stouter and with a decidedly straighter culmen than that of major. However, they pointed out that the differences were difficult to discern in the field. Table A4.1 gives Witherby et al.'s bill measurements. These data were reported again by Witherby et al. (1938-41). Table A4.1 suggests that the biometrical data were not significantly different, although this cannot be assessed as means and standard deviations (and indeed for females, sample sizes also) were not given.

By 1945 all standard works agreed that the British Great tit was distinct on bill characters only. However, none gave a statistical treatment in support of this. In size and colour, they agreed that there was no systematic difference. Harrison realised that no evidence had been put forward to support the existing taxonomy. In scanning through several series of newtoni and major skins, he noticed that the reported bill differences were not at all clear cut. Hence in 1945 he attempted to quantify this difference to assess the extent and consistency of the bill difference. I have already reported his methods and findings (see Introduction section 1.3). His data strongly supported the existing status of P.m.newtoni as a distinct subspecies although it is not clear how his Continental sample was selected.

Harrison (1945) clearly went to great lengths to standardise his data collection as far as was possible. He used only adult males. Care was taken

Table A4.1 Statistical ranges presented by Witherby **et al.** (1927, 1938-41) for specimens of **newtoni** and **major**. For males, n=12 of each race. All measurements are in mm.

Character	**P.m.newtoni**		**P.m.major**	
	male	female	male	female
Bill length	11 - 12.5	11 - 12.Ø	1Ø - 11	9.5 - 11
Bill width	5 - 6	4.5 - 5	4 - 5	4 - 4.5
Wing length	73 - 78	7Ø - 77	73 - 79	7Ø - 77

that all major specimens came from north and west of the Alps which he recognised as a possible barrier to gene flow (Harrison 1945). Hence we must assume that the selection of specimens and the data recording itself were carried out systematically. However, one criticism might be levelled against the 'bill coefficient' itself. Many, possibly the majority, of Great tit skins in the British Museum (Natural History) show considerable mandibular retraction. In most cases this has affected only the lower mandible, but in some, the upper mandible is depressed also. This displacement is caused by contraction of the jaw musculature on drying. The result is that in many cases, the bill is set open , and even when closed, the lower mandible may be retracted into an unnatural position. Hence, measurements of bill depth from these specimens would frequently be exagerated, and this might introduce uncontrollable bias. This source of bias should not influence bill length although I shall show later that bill length data from these specimens might also be at fault. In defence of his coefficient, Harrison states that much of its variation was due to variation in the bill breadth rather than the depth. Hence little bias should be expected from this source.

Snow (1953) examined systematically the morphological variation in several characters of the Great tit (see Introduction, section 1.3). Many characters showed clinal variation. Differences in body size (tarsus and wing length) and bill length between newtoni and major could all be attributed to clinal covariance with temperature. The colour variation described by Prazak was not substantiated. However, two British populations had rather deeper bills than should have been expected from their means of wing length, suggesting that the bills of British Great tits were indeed deeper than those of Continental major. Snow (1953) did not examine the curvature of the culmen. Nor did he refer to Harrison's (1945) paper, being concerned more with the

overall geographical trends in variation rather than with taxonomic peculiarities. The cline in body size suggested that British Great tits were larger on average than those on the Continent (Perrins 1979). This contradicts the type description. Further, if the morphological position of newtoni is consistent with the clinal trend of major, its subspecific status might be questioned.

Van Balen's (1967) demonstration that sexual dimorphism in body size varies among populations of the Great tit indicates that extreme caution should be exercised before taxonomic diagnosis may be made on the basis of such characters. British and Continental populations of the Great tit differ both behaviourally and ecologically in many respects such as the number of broods, the tendency to roost in nestboxes in winter (which may be only a local phenomenon), and the dynamics of immigration and emmigration (Perrins 1979). However, it is still not clear to what extent these result from local population differences (such as habitat, climate etc).

I have shown that bill characters in the Great tit are phenotypically plastic, and that the immediate environment has a profound influence. In the light of this, the subspecific status of P.m.newtoni should be re-evaluated. In this chapter, I shall compare the bills of Continental and British museum specimens. However, no definitive conclusion should be reached until more information is available on the factors influencing bill variation in continental populations.

Whatever the true taxonomic status of the British Great tit, it is unlikely that the type designated by Prazak is representative. Although this poses no taxonomic problem according to the rules of zoological nomenclature (ICZN), it would nevertheless be interesting to examine the bill of specimen number 10664 in Vienna.

A4.2. Methods.

The present analyses have two aims. First to identify to what extent geographical variation in bill characters might be influenced by the confounding effect of season arising from biases in the dates of collection among populations. Secondly, to re-examine bill variation in skins at the British Museum taking seasonal variation into account.

To determine whether temporal bias exists in the British Museum collection, I recorded the dates of collection of all Great tit skins from the following countries: Norway, Sweden, France, Holland, Denmark, Germany, Belgium, Scotland, England & Wales and Ireland. Sample sizes are shown in Table A4.2. To test for bias, a contingency table was set up in the form: months X countries and a chi-square value calculated for this. The results are presented in the next section and in Table A4.3.

To determine whether these differences in date could have a significant effect in a study of bill variation, I replaced (recoded) the month of collection of each bird with the mean value (for each character) for Wytham birds in that month (averaged over three years). The analyses were carried out separately for each sex. Table A4.4 shows the mean Wytham values used in this analysis. Hence a series of bill measurements in which variation was due only to season, was produced. Differences in bill measurements among countries were then tested by Kruskall-Wallis analysis of variance (not ANOVA, as an F_{max} test showed the data to be strongly heteroscedastic). The results are presented in section A4.3 and in Table A4.5.

Finally, I have re-examined the variation in culmen curvature in the Great tit. Forty full-grown males of newtoni and major (80 in all) were selected at

Table A4.2. Sample sizes available for tests of variation in the date of collection among skins of P. major at the British Museum (Natural History).

	Country	male	female	total
1	Norway	3	3	6
2	Sweden	16	3	19
3	France	36	21	57
4	Holland	4	3	7
5	Denmark	5	Ø	5
6	Germany	7	2	9
7	Belgium	1	2	3
8	England & Wales	91	51	142
9	Scotland	25	13	38
1Ø	Ireland	22	9	31
	TOTAL	189	129	317

Table A4.3 The distribution of Great tit skins at the British Museum (Natural History) by month. Countries are numbered as in follows: 1 Norway, 2 Sweden, 3 France, 4 Holland, 5 Denmark, 6 Germany, 7 Belgium, 8 England & Wales, 9 Scotland, 10 Ireland.

MALES

	COUNTRY									
MONTH	1	2	3	4	5	6	7	8	9	10
1	0	3	3	0	2	1	0	15	2	1
2	0	2	5	0	0	1	0	5	3	1
3	0	1	5	1	0	0	0	6	5	1
4	0	0	0	1	0	0	0	7	6	0
5	0	0	0	1	0	0	1	4	1	0
6	0	0	0	0	0	0	0	1	0	0
7	0	0	0	0	0	0	0	0	0	0
8	0	0	0	0	0	0	0	5	0	0
9	1	4	4	0	0	0	0	1	3	0
10	0	4	6	0	3	3	0	16	2	1
11	2	2	13	1	0	1	0	15	2	0
12	0	0	0	0	0	1	0	16	1	1

$X^2_{90}=185.35$
$P<0.001$

FEMALES

	COUNTRY									
MONTH	1	2	3	4	5	6	7	8	9	10
1	0	0	1	1	0	0	0	10	4	5
2	0	2	2	0	0	1	0	2	0	0
3	0	0	1	0	0	0	0	6	1	1
4	0	0	1	2	0	0	0	3	0	0
5	0	0	0	0	0	0	0	0	2	0
6	0	0	0	0	0	0	0	1	0	0
7	0	0	0	0	0	0	0	0	0	0
8	0	0	0	0	0	0	0	1	0	0
9	1	0	4	0	0	0	0	1	2	0
10	1	0	2	0	0	0	0	8	4	2
11	1	1	4	0	0	1	2	12	0	0
12	0	0	6	0	0	0	0	7	0	1

$X^2_{80}=113.58$
$P<0.01$

Table A4.4. Mean Wytham bill measurements used to 'generate' an artificial data set across countries (see text). Means are taken over three years and given in mm.

		MONTH											
Character.	**sex**	1	2	3	4	5	6	7	8	9	10	11	12
Bill len.	**male**	13.20	12.97	13.12	-	13.35	13.38	12.80	-	13.32	13.41	13.40	13.45
	fem.	13.16	12.93	13.08	12.80	13.55	13.69	13.67	-	13.43	13.25	13.21	13.16
Bill dep.	**male**	4.57	4.55	4.58	-	4.58	4.62	4.40	-	4.72	4.64	4.67	4.70
	fem.	4.33	4.40	4.45	4.30	4.36	4.44	4.55	-	4.20	4.39	4.36	4.40
Bill ind.	**male**	.347	.352	.349	-	.339	.345	.344	-	.355	.346	.349	.346
	fem.	.329	.340	.341	.336	.322	.325	.333	-	.313	.332	.330	.329

Table A4.5. Mean ± 1sd of bill depth and bill index by countries generated from an artificial data set based on seasonal variation only (see text). Data are for males only and Belgium was ommitted from the analyses as n=1. Means are in mm.

Country	n.	Bill depth	Bill index.
Norway	3	4.688 ± Ø.Ø25	Ø.351 ± Ø.ØØ35
Sweden	16	4.635 ± Ø.Ø63	Ø.349 ± Ø.ØØ37
France	36	4.633 ± Ø.Ø56	Ø.349 ± Ø.ØØ27
Holland	3	4.6Ø9 ± Ø.Ø56	Ø.346 ± Ø.ØØ58
Denmark	5	4.611 ± Ø.Ø33	Ø.346 ± Ø.ØØØ6
Germany	7	4.63Ø ± Ø.Ø53	Ø.347 ± Ø.ØØ23
Eng.& Wales	79	4.633 ± Ø.Ø54	Ø.347 ± Ø.ØØ3Ø
Scotland	19	4.617 ± Ø.Ø63	Ø.349 ± Ø.ØØ39
Ireland	21	4.582 ± Ø.Ø32	Ø.347 ± Ø.ØØ12
Kruskall-Wallis test (adjusted),		H = 22.31, P<Ø.Ø1	H = 31.79, P<Ø.ØØ1
ANOVA	$F_{8,18Ø}$	= 2.7Ø, P<Ø.Ø1	= 4.41, P<Ø.ØØ1

the British Museum. In the case of *newtoni* these were the first forty specimens examined in the collection. Similarly, for *major*, these comprised all French, Danish, Dutch and Belgian specimens. Hence specimens were not chosen specifically by the observer. The bill length of each skin was measured (as in the field) and the date of collection recorded. Each head was then photographed using the apparatus shown in plate 1 and described above. Bill curvature was then measured by the method described above for live birds (section 3.7). To test the repeatability of this method (since the measurement of curvature is to some extent subjective), seventeen randomly selected specimens were re-measured by a naive observer. No differences were found in the means of these two sets of observations and the data were themselves highly correlated (r_{15}=0.683, P<0.01). Hence, despite a high degree of error in its measurement, it should be sufficient to compare the means of two series of measurements. The bill curvature estimates of *major* and *newtoni* skins were compared within months by t test.

A4.3. Results.

Table A4.2 shows the sample sizes available for tests of date variation by countries among skins of P. major at the British Museum. Table A4.3 shows the distribution of these skins by months. The Chisquare values indicate that there was significant variation in the dates of collection among countries, in both sexes. For the sexes pooled, X^2_{90}=193.5 was highly significant (P<0.001). To test whether this could influence the observation of geographical variation (as suggested by Davis 1964), recoding was carried out (as described above). Table A4.4 shows the mean Wytham values used in this analysis. In females, no significant bill variation was observed across countries in these artificial data. However, in males, variation in both bill depth and bill index was highly significant as shown in Table A4.5.

Although Table A4.5 shows that apparent geographical variation among Great tit skins at the British Museum could have resulted from seasonal variation alone, it does not show that Harrison's data were necessarily biassed in that way. Although English and Welsh specimens differed significantly from Continental birds with respect to this artificial data set, the mean for Scottish birds did not. Clancey (1945) maintained that some Scottish populations of the Great tit might resemble major more closely than newtoni in bill depth. However, Harrison (1945b) presents data suggesting that Scottish birds had deeper bills on average than English so that the position is unclear. I have reanalysed Harrison's (1945) principal data set by ANOVA. Some 54.1% of variation in the bill coefficient could be attributed to racial (major or newtoni) differences ($F_{1,98}$=115.25, P<0.001). In a similar comparison of bill index in the artificial data set, only 9.4% could be so attributed ($F_{1,187}$=15.3, P<0.001). Although these are different

characters (bill coefficient and bill index), they share a common component (bill depth) and it is inconcievable that so great a difference in variation could have been caused by this. Hence although there is cause for concern, there is considerably more variation in Harrison's data than could be explained by seasonal bias.

Whitherby et al. (1938-41) and Bannerman (1953) state (without supporting data) that newtoni is longer billed than major. The mean bill length for the forty male specimens of newtoni measured at the British Museumwas 12.82±0.55 mm. That for major was 12.46±0.47 mm. This difference was highly significant (t_{78}=3.14, P<0.01). Only 11.2% of the total variation in bill length could be attributed to race. Table A4.6 gives the distribution by date of this photographed sample. The distributions for each race did not differ significantly. Table A4.7 shows the distributions of culmen curvature in these samples and Table A4.8 shows the mean bill curvature of specimens by month. As described by previous workers, the newtoni specimens showed a significantly straighter culmen on average. No significant seasonal variation in bill curvature was found across months in these two samples (Kruskall-Wallis test). Although the difference between the means of each race was not significant in every month, in six out of seven comparisons within months newtoni bill were less curved (Table A4.8). The probability of this occurring by chance is 0.055 (binomial test). Hence this analysis supports the views of previous workers that there are consistent differences between races although only 14.1% of the total variation in culmen curvature was attributable to race.

Table A4.6. The distribution of photographed specimens by months.

Month	P.m.major	P.m.newtoni	
1	4	3	
2	5	2	
3	5	7	
4	1	2	
5	1	3	
6	Ø	1	$X^2_{1Ø}$=17.68, n.s.
7	Ø	Ø	
8	1	Ø	
9	2	Ø	
1Ø	8	8	
11	13	6	
12	Ø	8	
Total	4Ø	4Ø	

Table A4.7. The frequency distributions of culmen curvature in two races of **P. major**. See section 3.7 for a description of the method.

% curvature.	**P.m.major**	**P.m.newtoni**
20	Ø	3
25	1	5
30	5	7
35	5	5
40	4	9
45	4	3
50	11	5
55	4	3
60	5	Ø
65	1	Ø

Table A4.8. Mean ± 1sd of % culmen curvature in two races of **P. major** grouped by months.

Month	**P.m.major**	n.	**P.m.newtoni**	n.	t	d.f	P.
1	50.97 ± 2.48	4	33.20 ± 8.69	3	3.439	5	<0.02
2	41.38 ±12.78	5	32.41 ± 0.94	2	1.558	5	n.s.
3	44.84 ±11.04	5	38.67 ±10.59	7	0.971	10	n.s.
4	34.71 ± 0.00	1	46.83 ± 4.49	2	-3.816	1	n.s.
5	59.35 ± 0.00	1	37.83 ±17.76	3	2.099	2	n.s.
6	-	0	21.90 ± 0.00	1	-	-	-
7	-	0	-	0	-	-	-
8	50.00 ± 0.00	1	-	0	-	-	-
9	52.91 ± 6.94	2	-	0	-	-	-
10	50.35 ±10.40	8	36.32 ±10.16	8	2.729	14	<0.02
11	40.65 ± 7.71	13	37.50 ± 7.40	6	0.850	17	n.s.
12	-	0	38.99 ±10.41	8	-	-	-
All	45.40 ± 10.42	40	37.29 ± 9.86	40	3.14	78	<0.01

Δ4.4. Discussion.

In this chapter I have sought to re-examine the existing taxonomy of the British Great tit, and to warn taxonomists of the dangers associated with the use of bill characters in infra-specific taxonomy. Without a knowledge of the dynamics of bill size determination in the populations from which specimens were drawn, museum collections present a wealth of uncontrolled (and uncontrollable) sources of bias. A comparison between the mean bill length of the forty British skins in the British Museum and that of males in the Wytham population shows that Wytham bills are significantly longer ($t_{886}=5.53$, $P<0.001$). This might derive partly from the strong bias in favour of winter collection in the museum specimens, but other causes such as *post mortem* shrinkage (although unlikely in a passerine bill) should not be ruled out.

While museum specimens did indeed show geographical variation in the manner described by previous workers, only about 10-15% of the total variation in racially diagnostic characters could be attributed to this in the present study. I have already shown that bill variation within populations of the Great tit may be considerable. For eighty bill lengths measured at the British Museum, the coefficient of variation was 4.25% (mean = 12.64 $\pm$ 0.54 mm). This was significantly greater than the equivalent value shown in Table 3.1 of 3.28% for Wytham males (Variance ratio of logged data, $F_{79,847}=1.655$, $P<0.01$). Since it is not yet known to what extent, populations within a 'subspecies' may differ in these characters, one cannot say whether this is a sufficient difference upon which to base a taxonomic distinction. Until a single observer has the opportunity to make comparable observations in both continental Europe and Britain, the validity of subspecific status for *P. m. newtoni* defined solely upon bill characters, must be in question.

Appendix 5.

Appendix 5. The derivation of a mathematical model to predict the asymptotic prey size diversity associated with two maximally separated prey size distributions resulting from a correlation between bill length and prey size for two parent birds with different bill lengths. Credit for this derivation goes to Dr A. Grafen of the Department of Zoology, Oxford, and to whom I give grateful acknowledgement.

For a single prey size distribution (eg: normal).

$\bar{H} = \Sigma pi \ln pi$ where pi is the probability of drawing an item of size i.

Therefore for two equal prey size distributions, that is for two distributions associated with bill lengths of the two parents, the diversity of prey size is as follows:

each category has pi/2, but occurs twice, therefore the new $\bar{H}$

$= - \Sigma(pi/2)\ln(pi/2) - \Sigma(pi/2)\ln(pi/2)$

$= - \Sigma pi \ln(pi/2)$

$= - \Sigma pi[\ln pi - \ln 2]$

$= - \Sigma pi \ln pi + \Sigma pi \ln 2$

$=(\bar{H}$ for one distribution$) + (\ln 2)\Sigma pi$, but $\Sigma pi = 1$,

Therefore the diversity of two distributions $= \bar{H} + \ln 2$

ln2 is 0.693, and in the present model (chapter 5), the $\bar{H}$ value for one distribution is given by the intercept of Figure 5.2 which is 1.14.

Therefore the theoretical asymptotic value for two distributions is 1.14 + 0.693 = 1.83 .