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HERITABILITY OF ECOLOGICALLY IMPORTANT TRAITS IN THE GREAT TIT

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This paper is dedicated to the memory of Dr. H. N. Kluyver with whom the possibility of this study was discussed in 1971

CONTENTS

1. INTRODUCTION

Ecologically important characters in birds, such as clutch size, date of laying and body size, vary within and between populations and species. The mean values of these characters are considered to be fixed by natural selection on values ensuring a maximum reproductive output over a life-time. For clutch size this implies that more eggs may result in less offspring. Lack (1954a) showed that mean clutch size is fixed at an optimal number: when this number is exceeded the number of young dying from starvation is so large that the productivity of the brood decreases.

However, natural selection will only result in evolutionary adaptation if genetic variation is available. Data on the amount of genetic variation in these ecologically important characters were not available. Concepts of adaptation processes were largely based on general ideas about genetic variation in natural populations.

Until recently two rival theories on the organisation of genetic variability in populations were vigorously discussed. The classical theory of genetic variation states that individuals in natural populations are essentially homozygous for wild-type genes (see Muller 1950). Only a few gene loci would be heterozygous for deleterious recessive genes, which could be favoured by selection only after a change in environmental conditions. This theory implies that adaptive evolutionary change will be a long term process. This is reflected in Lack's (1965) warning that bird populations which live in an environment that had changed in recent ages, might not yet have evolved to the new optimum values.

However, already in 1929 Sewall Wright suggested that the genetic structure of populations was in a "shifting state of balance" (Wright 1960). Individuals in wild populations would be heterozygous on the majority of their gene loci. On each locus many so-called wild-type isoalleles would be found. This view gained strength during the fifties when it was found that artificial selections for measurable traits in livestock and laboratory animals gave almost always immediate results, indicating a large reservoir of genetic variability (Falconer 1960). Moreover, with special genetic techniques available in Drosophila it was shown that in wild populations recessive genetic factors causing lethality or sterility are present in high frequencies (Dobzhansky 1970). Since 1965 it has been shown using electrophoretic techniques that enzymes and other proteins show much genetic variation, indicating that in wild populations a considerable part of the genome is heterozygous (Lewontin 1974). However, with only a few exceptions such as alcoholdehydrogenase and amylase in *Drosophila melanogaster* (Van Delden *et al.* 1978, Hoorn & Scharloo 1979) the selective significance of these enzyme differences is not known. The theory that most of the enzyme differences are selectively neutral has still much support (Ewens 1977).

Therefore, the theory that the mean values of ecologically important characters are established

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by natural selection can only be assessed by a direct study of their genetic variation in natural populations. In contrast to the simple Mendelian genetics of enzyme variation, the genetics of measurable characters is complex. Many genes are involved and environmental factors have important effects. Therefore the statistical methods of quantitative genetics have to be applied. These were developed for animal breeding and have often been used for quantitative traits in laboratory animals.

During the longterm study of several populations of the Great Tit (*Parus major*) at the Institute for Ecological Research at Arnhem, all nestlings have been ringed, while nearly all parents were caught and identified on the nest. This allows the construction of family trees necessary for the application of the methods of quantitative genetics. All results in this paper come from the main study area, the Hoge Veluwe. A description of this area and the methods used is given by Van Balen (1973).

In this paper we will first examine the methods used to establish the relative contribution of genetic variation. Then we will give estimates for four different traits: clutch size, date of laying, egg dimensions and body size. Further we will look at the selection pressures on clutch size and date of laying and their possible contribution to the preservation of genetic variation.

2. METHODS USED IN QUANTITIVE GENETICS

Studying the variation of a quantitative character such as body size in a population, it is assumed that there are two groups of causes for this variation: genetic differences and environmental differences. The first aim is to divide the total or phenotypic variance (V_p) into its components, the genetic variance (V_g) and the environmental variance (V_e). If it were possible to subject all individuals to exactly the same environment (from conception to death), all observed variation would be due to differences in genes. On the other hand, the variation observed between individuals that are genetically identical must be due to differences in the environment. In less extreme situations in which both environmental and genetic variance contribute to the phenotypic variance, a partition of the total variance must be made. Heredity implies that offspring resemble their parents. In Great Tits there is a positive regression of the mean body weight of females on the mean value of its parents (Fig. 2a). Such a relation can be evaluated in terms of genetic and environmental variance.

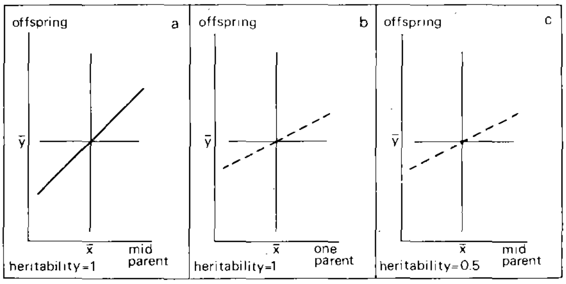

Fig. 1. Theoretical diagrams of regression of mean offspring values on parental values. In a) and c) the offspring values are plotted against the midparent value, in b) against a single parent. In a) and b) all variation is genetic, while in c) only half the phenotypic variation is genetic. In a) and c) the slope of the regression is equal to the heritability, while in b) the slope represents half the heritability.

If all differences between the parents were genetic the offspring-value would be identical to the midparent-value (Fig. 1a). If these values of offspring were plotted against the measurements of one parent, only half the difference between this parent and the population mean will be found in the mean of its offspring (Fig. 1b, Fig. 2b). But this will only hold when there is no correlation between the values of the two parents. If this correlation is complete, that is male and female values are equal, the same relation will be found as in Fig. 1a. If only half of the phenotypic variance is genetic and the other half is caused by environmental differences the slope of the line representing the relation between the mean value of offspring and midparent will be 0.5 (Fig. 1c).

A parameter indicating the proportion of the total variance which is genetic is the heritability:

$$h^2 = V_g / V_p$$

The heritability is equal to the slope of the regression lines of offspring on midparent value. Complications may arise from assortative mating, that is, males and females do not mate randomly but choose partners with a similar value for the character concerned.

Further, likeness of offspring and parents is not necessarily a consequence of common genes, but can also be a consequence of living in a common environment. This would mean that genotypes are not distributed randomly over the environment. This difficulty can be forestalled in work on laboratory animals, but is likely to be present in natural populations. It is one of the most serious criticisms of the use of these methods in human populations, in particular in relation to mental abilities such as intelligence.

In birds for instance, one could imagine that a large male has an advantage in occupying a territory with good feeding conditions, which would provide his young with relatively much food, enabling them to grow to a large size without genes being involved here. In some cases we succeeded in separating this kind of effect from real genetic ones and we could show that this influence is smaller than the contribution from genes.

In this respect the repeatability, that is the constancy in performance of one individual is important. The environmental variance (V_e) is further divided into two components, the special environmental variance (V_{es}) and the general environmental variance (V_{eg}). The special environmental variance is computed from the difference between measurements on the same individual, *e.g.* differences in size between clutches of the same individual. The general environmental variance concerns differences between individuals, such as the lasting effect of conditions during growth. In the repeatability ($r = (V_g + V_{eg}) / V_p$) this general environmental variance cannot be separated from the genetic variance. For clutch size for instance it is possible to calculate the repeatability of the subsequent partners of one male. Male Great Tits will almost always occupy the same territory. If the repeatability in females was mainly due to the occupation of the same territory, the repeatability in clutch size for the different partners of one male would be similar.

3. HERITABILITY ESTIMATES

3.1. BODY WEIGHT

It is clear that body weight will be influenced by environmental factors. The body size of adults will be affected by the food obtained when growing up in the nest and the body weight will change continuously depending on the food supply. Do genetic differences contribute to the total variation in body weight? For this analysis we used the mean of all weights of an individual taken outside the breeding and moulting season, with the condition that at least three measurements must be available.

Table 1. Heritability (mean ± S.E.) of mean body weight. Only individuals of which at least three weights were taken outside the breeding and moulting season have been used. No corrections for age, sex, time of day or year were made. Data from Hoge Veluwe 1955-1978

	Mother	Father	Mid-parent
Daughter	0.63 ± 0.15	0.72 ± 0.14	0.68 ± 0.10
	n = 112	n = 137	n = 90
Son	0.65 ± 0.13	0.59 ± 0.11	0.50 ± 0.09
	n = 181	n = 255	n = 146

Four different estimates based on regressions of offspring on one parent were made (Table 1). Doubling the regression coefficients gave estimates of heritability, which can be compared with heritabilities obtained as regression on midparent values (Fig. 2). The good agreement between these estimates shows that assortative mating is not important for this character.

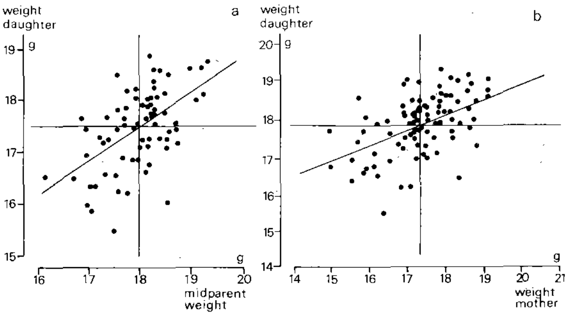

Fig. 2. Heritability of body weight. a) Mean body weight of females is plotted against the mid-parent value, and b) against the value of the mother (see also Table 1.).

These data suggest that more than half of the deviation in body weight from the population mean can be predicted from knowledge about the body weight of the parents. This is a surprisingly high value.

3.2. FEMALE CHARACTERS

Characters such as clutch size, date of laying and egg dimensions are female characters. Our results will show that they depend to a large extent on the female genotype. In particular the first two characters are affected by environmental factors and it could have been expected that males had an influence *e.g.* by providing food or by their mating behaviour.

3.3. CLUTCH SIZE

In Table 2 repeatability values are given which indicate a constancy in clutch size of individual females. This can be caused by constancy in genes and/or constancy in environment, because Great Tits tend to live in the same place during their breeding life. When differences in environment would have been important, it must be expected that the repeatability in clutch size for males mated with different females would approach the repeatability for females. Although this repeatability is different from zero, its value is less than the female value. This suggests that genes are predominantly responsible for the constancy in laying.

Table 2. Repeatability (r) of clutch size in first clutches. Data from Hoge Veluwe 1955-1978. n is number of individuals

	n	r	95% conf. limits
♀ total	357	0.42	0.32- 0.50
♀ with diff. ♂	234	0.45	0.34- 0.55
♀ + ♂ pairs	122	0.30	0.13- 0.45
♂ with diff. ♀	218	0.13	0.01- 0.26
♂ total	304	0.19	0.07- 0.29

Table 3. Heritability (mean ± S.E.) of clutch size in first clutches. Heritabilities were obtained by multiplying the regression coefficients and standard errors by 2 for parent-offspring values and by 4 for grandparent-grandchild comparisons. Comparisons were only made between members of the same sex. Data from Hoge Veluwe 1955-1978

	♀	♂
Parent-child	0.37 ± 0.12 (n=301)	0.05 ± 0.11 (n=419)
Maternal grandparent-grandchild	0.38 ± 0.56 (n= 99)	-0.04 ± 0.36 (n=138)
Paternal grandparent-grandchild	0.68 ± 0.38 (n=136)	0.05 ± 0.31 (n=175)

This is supported by the regression of offspring on parents (Table 3). The mother-daughter regression is high and gives a heritability estimate of 0.37, the father-son regression is low and insignificant. This supports the notion that the female genotype affects clutch size and that the male genotype is not important in this respect. Moreover, these results indicate that it is unlikely that the resemblance is caused by identical environments. If the resemblance was caused by a common environment, an effect through the male line would be more likely, because males tend to breed closer to their place of birth than females.

Although the male genotype does not affect clutch size, males transmit genes for clutch size to their daughters. This is revealed by the regression coefficients of granddaughters, both on maternal grandmother and on paternal grandmother, while the similar regression in the male line is practically zero. Although the standard errors are high, these values are suggestive.

3.4. EGG DIMENSIONS

During 1977 and 1978 all eggs in the study area were measured. Table 4 summarises some preliminary results. All data are based on mean values of all eggs in a clutch. All four traits, length, breadth, volume and shape show a similar

Table 4. Repeatibilities and heritabilities of egg dimensions. The volume was calculated as $.495 \times l \times b^2$. (Van Noordwijk *et al.*, in prep.). All female repeatibilities are significant at 1%, none of the male repeatibilities is significant at 5%. Heritabilities are given with S.E. Data from Hoge Veluwe 1977-1978

	Length	Breadth	Volume (calculated)	Shape (length/breadth)
Repeatability first '77-first '78 ♀ (n=32)	0.79	0.59	0.59	0.88
Repeatability first '77-first '78 ♂ with diff. ♀ (n=18)	0.08	0.19	0.12	0.13
Heritability based on mother-daughter regression (n=53)	0.53±0.28	0.80±0.26	0.61±0.25	0.95±0.35
Repeatability first-second 1977 ♀ (n=27)	0.68	0.62	0.57	0.79
Repeatability first-second 1978 ♀ (n=26)	0.80	0.72	0.67	0.93

pattern: a high repeatability in females, a much lower repeatability in males (with different partners) and heritability values calculated from mother-daughter regressions that are similar to the female repeatabilities. The data suggest that more than half of the total variance in these characters is genetic.

Environmental effects can only be small: repeatabilities for clutches sired by males with different partners are much lower than the female repeatabilities. This is also apparent from the high repeatabilities found between first and second broods. The environmental conditions for a female when forming her first clutch and her second clutch are drastically different. Nevertheless the repeatability for first to second clutch is of the same magnitude as that for the first clutches from different years. The repeatability for egg-shape is so high that it might be used as a criterion whether or not an abandoned clutch and a repeat clutch are likely to have been produced by the same female.

3.5. DATE OF LAYING

There is considerable variation in date of laying between years. This suggests that the influence of environmental factors will be large. Källander (1974) has shown that by supplementing the amount of insect food, the onset of laying in his population of Great Tits could be advanced by almost a week.

The onset of the breeding season is correlated with air temperature in late winter and early spring (Kluyver 1952). The question whether this acts directly on the birds or through an effect on the growth of the insects on which the birds feed, has not been answered. It is likely that the same mechanisms that cause the difference between years will also contribute to the differences between individuals within years. Although it is evident that differences in the amount of available food will lead to differences in date of laying, it is also quite possible that individuals in exactly the same environment would still show variation. This variation could be attributed to *e.g.* differences in the efficiency of foraging or of metabolism. Such differences could be genetic.

In Table 5 the repeatability values are given for both the absolute date of laying and for the date relative to the median date of all first clutches in that particular year. In calculating parent-offspring regressions a problem arises, because in a substantial part of the data parents and offspring were breeding in the same year. In those years that were extremely early or extremely late, this will add substantially to their likeness. This is a clear example, where (with respect to time) genotypes that are to be compared, are not randomly distributed over environments. In order to eliminate this effect a control group was created. All offspring were compared with a parent other than their own, that lived contemporaneously with their true parent. The difference between the regression of offspring on true parents and on "control-parents" was taken as an estimate of heritability.

The standard error of the difference is larger than that of the original regressions. As is to be expected the effect of this correction was much larger on the absolute dates than it was on the relative dates. For a more detailed discussion see Van Noordwijk *et al.* (in prep.). Regarding both the repeatability and the heritability estimates there seems again to be no effect of the male. An overall estimate of female heritability is approximately 30 per cent.

Table 5. Repeatability (upper part) and heritability (mean ± S.E.) of date of first egg laying of first clutches (* = $P < 0.05$, ** = $P < 0.01$). Data from Hoge Veluwe 1955-1979

	N clutches	N individuals	Calendar dates	Relative dates
♀ total	896	357	0.26**	0.27**
♀ with diff. partners	535	234	0.28**	0.26**
♀ + ♂ pairs	267	122	0.34**	0.24**
♂ with diff. partners	298	218	0.07	0.02
♂ total	741	304	0.13*	0.06
♀ h^2 from mother-daughter regression		301	0.21 ± 0.19	0.40* ± 0.18
♂ h^2 from father-son regression		414	0.02 ± 0.16	0.04 ± 0.16

4. SELECTION

4.1. SELECTION FOR DATE OF LAYING

Selection is present when different phenotypes make different contributions to the next generation. If we group our data according to phenotype, we can then simply count for each group the number of offspring in the next generation. We made such a count over a complete annual cycle starting from breeding adults: their contribution to the recruitment into the next years breeding population is determined. In the Great Tit a life cycle can be completed in one year. Such a measurement over the whole life-cycle is important, because it measures the real contribution to the next generation. In most studies selection has been followed only over a part of the life-cycle (Lack 1966, Perrins 1979). In particular the use of recaptures after at least three months may introduce an error. It is conceivable that a proportion of the population disperses to other areas in winter and then returns in spring. This group would be underrepresented in the autumn and winter recaptures.

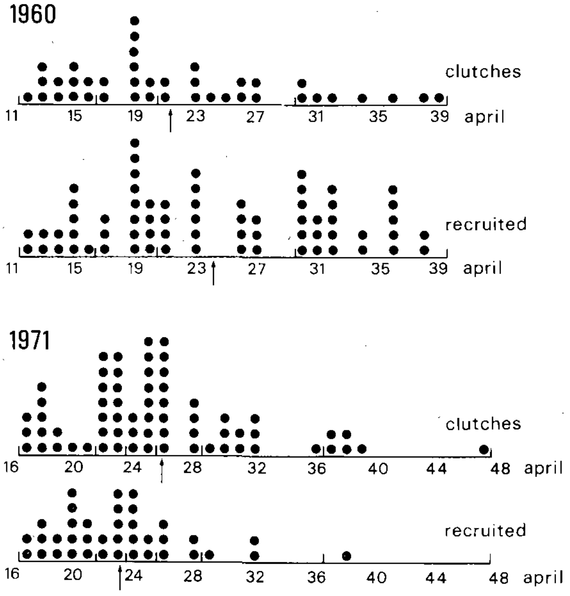

Fig. 3. Examples of selection on date of laying for two years. Data from Hoge Veluwe. In both years the upper diagram gives the date of laying for all first clutches. The lower diagram gives all individuals (born in a clutch of which the first egg date is indicated), which were observed breeding in a subsequent year. The means are indicated by arrows. The difference between the means is used as a measurement of selection intensity.

In these analyses we will concentrate on the recruitment from first clutches. Fig. 3 shows for two years the distribution of all first clutches with respect to date of laying. The numbers of fledglings from these clutches that were recorded as breeding birds in later years are also given. The arrows indicate the means of the distributions. There are differences of a few days between the mean dates of clutches and recruits. This difference can be used as an overall estimate of selection in a particular year.

The question arises at what stage this selection occurs. To answer this question, the clutches were combined in groups of about ten clutches (as indicated in Fig. 3), and the mean clutch size, the mean number of fledglings and the recruitment per group were calculated. In Fig. 4 these values are given for 1960 and 1971. In the graphs at the bottom it can be seen that in 1960 the late first clutches were most productive, while in 1971 the earliest were. In the upper graphs it can be seen that there were no differences in the number of fledglings per clutch in 1960, while there is a slight decline with time in 1971. The most important effect comes in both years from the rate of recruitment per fledgling. This leads to the conclusion that selection for date of laying takes mainly place after fledging. It should be noted that the recruitment from repeat and second clutches is relatively high in those

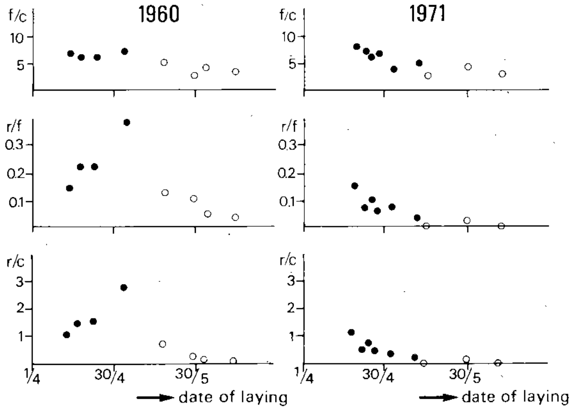

Fig. 4. Selection for date of laying. Clutches were taken together in groups of about ten each (as indicated in Fig. 3). For both years the number of fledglings per clutch (f/c), the number of recruits per fledling (r/f) and the number of recruits per clutch (r/c) are given. Solid dots = first clutches, open circle = repeat or second clutches, given for comparison.

years when the late first clutches do best. There seems to be a continuity in time in the recruitment success irrespective of the type of clutch.

Before presenting data for all years with their selection differentials, we should look at the relation between selection differential, heritability and the selection response (the change in population mean as a result of selection). In Fig. 5 the values of the parents are given on the abcissa and the values for the offspring on the ordinate, the slope of the regression line gives the heritability of the trait (0.4 in this example). If there is selection favouring parents with high values (represented by black dots), then the difference in mean between this group and the total population is the selection differential (S). What is the expected value of the offspring from these parents? The expected mean of the offspring is equal to the expected offspring value for parents with a value equal to the mean of the selected parents. The difference between the mean of the selected offspring and the mean of all offspring is the selection response (R). Hence the selection response (R) is equal to the product of heritability and selection differential (R = $h^2 . S$). This response to selection is evolution, if it is taking place on the proper time scale.

Table 6 gives the selection differentials for date of laying for all years with sufficient data. In many years this differential is very low, but in some years the selection differential may be up to about two days, *i.e.* about 0.4 standard deviations

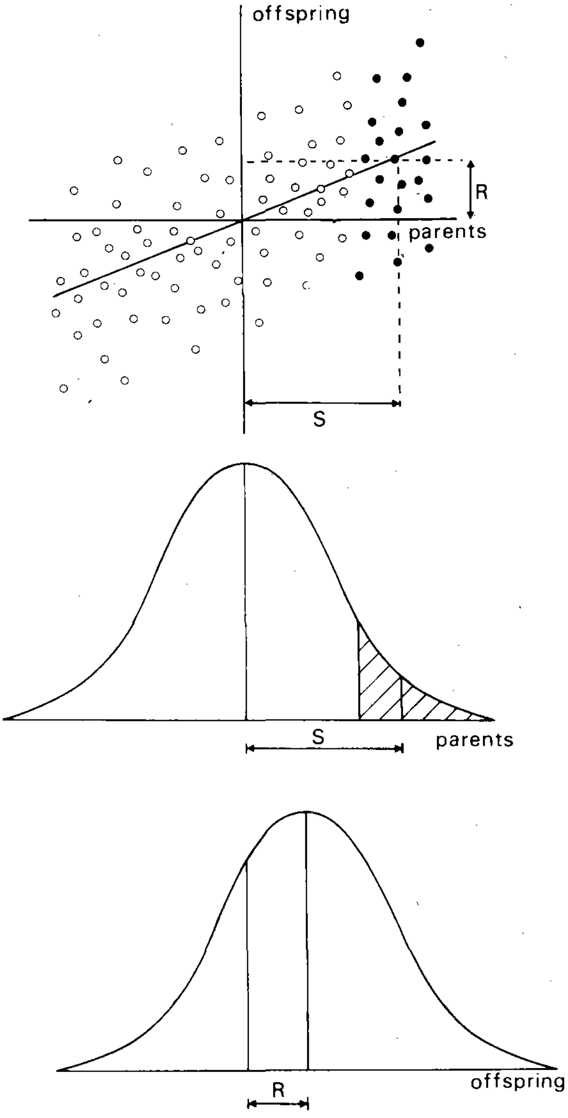

Fig. 5. The relation between heritability, selection and change in population mean. In the upper graph the values of the offspring are plotted against the mid-parent value. We suppose that only parents with a high value were allowed to contribute to the next generation (the black dots). The difference between the mean of the base population and the mean of the selected group is the selection differential S. The resulting difference between the offspring of selected parents and that of all offspring, the response to selection R, is the product of the heritability (h^2) and S (after Falconer 1960).

Table 6. Weighted selection differentials for date of laying and clutch size. Data from Hoge Veluwe 1955-1978

Year	Number of clutches	Number of recruits	Selection differential date of laying (days)	Selection differential clutch size (eggs)
1958	29	28	-0.52	-0.13
1959	77	21	-1.32	-0.25
1960	40	67	2.14	0.18
1961	116	10	-0.24	-0.47
1964	24	29	-0.92	0.35
1965	116	28	1.58	0.49
1966	78	64	1.86	0.08
1969	99	52	-0.30	0.14
1970	89	118	0.11	0.11
1971	65	38	-2.55	0.15
1972	84	21	0.93	-0.18
1973	64	21	1.14	0.06
1974	57	39	-0.76	0.04
1975	138	31	1.13	-0.02
1976	114	83	0.16	0.10
1977	145	43	-0.13	0.21
Mean			0.14	0.05
Mean of absolute values			0.99	0.19

of the original distribution. Although the average magnitude of the selection differential (that is irrespective of sign) is about one day, the net selection over all these years together (*i.e.* the average selection multiplied by the number of years) is smaller than some of the selection differentials observed in a single year. The question arises whether these differences are real or just chance effects due to the small numbers. The hypothesis that there is no selection can be tested by calculating a Chi square within each year, and by then combining the P-values. We obtained a low probability (P=0.007) for this null-hypothesis. So there is selection at least in some years, but without a directed change.

4.2. SELECTION FOR CLUTCH SIZE

Although there is some correlation between date of laying and clutch size in the Hoge Veluwe data, we assume selection for clutch size to be independent from that for date of laying. In both years shown in Fig. 6 the number of fledglings per clutch increases with clutch size. This is true for nearly all years. However, the recruitment per fledgling decreases with increasing clutch size. The resulting recruitment per clutch is variable. This can best be seen from the averages of the regression coefficients in individual years for these rates on clutch size, as given in Table 7. It can be seen that only the regression coefficients for the number fledged per clutch and for the recruitment per fledgling are significantly different from zero. The amount of selection measured as a selection differential is given in the last column of Table 6. Compared to the values for date of laying, the net selection over 16 years is somewhat larger, *viz.* it is larger than any selection differential found in a single year.

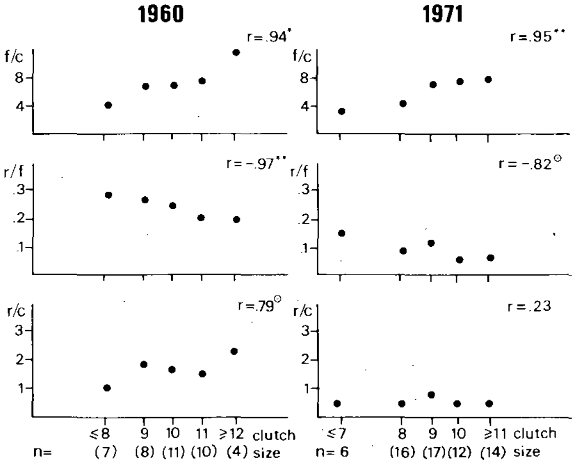

Fig. 6. Selection for clutch size. For explanation see legend Fig. 4.

Table 7. Selection for clutch size. Means of the regression coefficients of number of fledglings per clutch, recruits per fledgling and recruits per clutch, on clutch size in individual years. Data from Hoge Veluwe 1955-1978

Fledglings/clutch =	0.636	(± 0.087)	clutch size + constant
Recruits/fledgling =	-0.0076	(± 0.0027)	clutch size + constant
Recruits/clutch =	0.0215	(± 0.0165)	clutch size + constant

It is hardly possible to group clutch size in a few groups with roughly equal numbers so that a test whether these observed selection differentials are larger than could be expected due to chance, was not performed. It is doubtful whether a result as significant as that for date of laying would have been obtained.

5. DISCUSSION

Several studies have recently revealed the existence of genetic variation in quantitative characters in populations of passerine birds. Some of the values obtained in studies of the Great Tit are summarized in Table 8. Bearing in mind that there are some differences in the methods used, the over-all agreement is surprisingly good. Moreover, Boag & Grant (1978) have reported extremely high heritabilities for bill measurements and high values for body size in *Geospiza fortis*. Smith & Zach (1979) found considerable genetic variation for the same traits in a Song Sparrow (*Melospiza melodia*) population, although their heritability values are somewhat lower.

However, it must be emphasized that little attention has been paid to the possibility of offspring-parent resemblance through a correlation in environment between parents and offspring. For breeding parameters, which are properties of females, *e.g.* clutch size, this can be done through male comparisons from which the possibility of covariance through correlated adult environments can be estimated. In the work reported here, the results show that these environmental

Table 8. A comparison of heritability and repeatability values from this study with those from other studies on the Great Tit. Heritabilities are, except for body size, based on mother-daughter regressions, but there are some differences in the methods used

	h²		repeatability	
Clutch size				
Perrins & Jones (1974) 1)	0.48	n = 256 a	0.51	n = 267 b
This study	0.37	n = 301 b	0.45	n = 234 b
Onset of laying				
Jones (1973) 1)	0.14	n = 359 a	0.34	n = 44 b
This study	0.30	n = 301 b	0.27	n = 234 b
Egg size				
Weight, Jones (1973)	0.72	n = 81	0.72	n = 84
Volume, Ojanen *et al.* (1979)	0.86	n = 45 b	0.58	n = 421 b
Volume, this study	0.58	n = 51 b	0.61	n = 32 b
Body size				
Tarsus length, Garnett (1976)	0.76	n = 61 b	0.92	n = 34 b
Weight, this study	0.59	n = 236 b		

a) numbers refer to clutch by clutch comparisons
b) numbers refer to average values per individual
1) Jones (1973) and Perrins & Jones (1974) have first eliminated the effects of age, year and area.

causes of resemblance can not be very important.

From the existence of genetic variation we must conclude that directional selection will result in a change in the population mean. If there was a moderate selection pressure, *e.g.* a selection differential of about one standard deviation, this will lead to very rapid changes. For clutch size, a heritability of 0.4, a standard deviation of about 1.5 eggs and selection on one parent only, gives a change of 1.5 × 0.4 × 0.5 = 0.3 eggs in the mean clutch size of the population in a single generation. With an average generation time of about two years this might mean a change of 1.5 eggs in average clutch size in a decade. Similarly for date of laying we come to a value of 0.2 × 5 × 0.5 = 0.5 days per generation or 1 day per generation from the heritability of relative date of laying. This is about five days per decade.

One must be rather careful with such extrapolations from heritabilities, but in experimental situations it has been shown that in most instances extrapolations up to about ten generations are valid (Falconer 1960). However, this depends on the validity of the heritability obtained and on the recent history of selection. If a character has recently been subjected to continuous directional selection, it is possible that although genetic variation is still present, no further response to selection can be obtained (Robertson 1955). We have shown that at present there is no directional selection for date of laying or clutch size. Therefore, it is unlikely that this potential complication affects our extrapolations.

Not every heritability is equally suitable for the prediction of response to selection. Let us suppose that age has a strong effect on clutch size. If this effect is similar for all genotypes, we could make a better prediction of offspring values by calculating a heritability of performance corrected for age. Indeed if our aim was to explain the observed variation, it would be sensible to eliminate all sources of known environmental variance and calculate a heritability in the remaining variance. However, the effect of age would lead to a situation in which the same genes, transmitted at different ages of the mother, are subjected to the different forces of selection, that are associated with the differences in phenotypic value. The criterion to be used in deciding whether or not to exclude a part of the variation is its significance with respect to selection. Thus if we assume that selection for date of laying is in fact selection within the population, it is probably more relevant to know probable. To explain all of this change, only a cent of the population fledging within a given year irrespective of the actual date. Then the heritable part of the variance in laying date within a year is the relevant parameter. In the other traits, no corrections were made. If anything, this will make our predicted response to selection slightly too low.

Do such changes really occur? Beintema (1978) has reported systematic changes in the dates of laying of several species of waders breeding in grasslands over the past 50 years in the Netherlands. There are several ways in which these changes might be a consequence of changes in agricultural methods. However the fact that the change is largest in the Black-tailed Godwit (*Limosa limosa*), starting laying about a fortnight earlier nowadays, while this species is known to be the most sensitive to loss of young through mowing may indicate that a change in genetic composition through selection is quite problable. To explain all of this change, only a heritability of about 0.3 and a consistent selection differential of a few days are needed. Lack (1947-1948) has reported that in the first few years after its introduction into England the clutch size of Little Owl (*Athene noctua*) was similar to that in its original area, but soon afterwards declined. This indicates that it was probably not an environmental effect, but a change in genetic composition. Dhondt *et al.* (1979) have shown a significant decreasing trend in the mean body size of the Great Tit in their study areas over 14 years. They argue that the responsible selection is an effect of population density brought about by their provisioning of ample nest sites and thus compensating the effects of forest management. Conspicuous adaptive differentiation in colour and size has occurred in the House Sparrow (*Passer domesticus*) in North America since its introduction in the middle of the nineteenth century (Johnston & Selander 1964). However, the genetic basis of these changes was not analyzed. In all these examples a change in environment has been followed by a change in phenotype, which has been made possible by the existence of genetic variation. This raises the question how this genetic variation is preserved when there is no change in habitat. Our results suggest that selection favours different values for clutch size and for date of laying in different years. Lack showed such varying selection for clutch size over a small part of the life cycle in the Swift (*Apus apus*) and the Great Tit and suggested that such selection could be responsible for the existence of variation in this character (Lack 1954b, 1966, but see Perrins & Moss 1975).

The question of whether varying selection leads to stable polymorphism has been studied in several models (Roughgarden 1979). Both with selection varying in time and selection varying in space, there are conditions under which variation is preserved. The relative importance of this mechanism for the maintenance of genetic variation in populations is not clear.

The results of this study point to the availability of a large reservoir of genetic variation. The operation of selection on such a reservoir can result in rapid changes of mean values. Differences in body size, clutch size, egg size and date of laying as found between subspecies and related species, can be brought about within decades, if the potential rates of change at moderate selection pressures are realized.

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7. SUMMARY

A central theme of evolutionary ecology is that presently observed traits can be understood as the result of natural selection. Clutch size and data of laying are thought to be such that maximum productivity is ensured. Attributing this role to natural selection implies the availability of genetic variation for these traits.

It appears that about 40 per cent of all variation in the size of first clutches is genetic. About 30 per cent of the variation in date of laying can be attributed to genetic causes, and for several egg characteristics the relative contribution of genetic variation is 50—70 per cent, while about 60 per cent of average body weight variation is genetic.

It is shown that both for clutch size and for relative date of laying the optimal value of these characters is not constant. In some years small clutches are optimal, in other years large clutches contribute more to the next generation. These differences arise mostly after fledging. A similar pattern is found for date of laying. The existence of varying optima can contribute to the preservation of genetic variation.

The potential rate of evolutionary change is high. Further, no single optimum value exists for clutch size or date of laying. The variation probably mirrors the range of values that are at some moment, or at some place more productive than others.

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