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2) GENETIC AND ENVIRONMENTAL VARIATION IN  
CLUTCH SIZE OF THE GREAT TIT (*Parus major*)

by

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SUMMARY

An analysis is made of genetic and non-genetic components in the number of eggs in the completed first clutch of the Great Tit.

- 1) It is doubtful whether a causal relation between density and clutch size exists.
- 2) There is hardly a systematic effect of age on clutch size.
- 3) There is an annual variation in clutch size with similar changes in individual females in the same population, but it is hardly correlated between populations. This emphasizes a lack of genotype-environment interaction.
- 4) Within populations there is no detectable variation in clutch size that can be attributed to differences in habitat quality.
- 5) About 40% of the total phenotypic variation in clutch size is genetic variation. Several ways of eliminating a possible resemblance through correlated environments yield the same result.
- 6) Selection for clutch size is demonstrated in several years.
- 7) The implications for rapid evolutionary change in mean clutch size are discussed.

INTRODUCTION

In many species of birds clutch size is variable. A part of this variability is caused by differences in clutch size between populations in different areas or habitats, between years in the same population, between age-classes or between groups with a difference in territorial status. However, large differences are also found between individuals similar in all these respects.

The question arises whether genetic differences between individuals contribute to the variability in clutch size. In his review on the determination of clutch size in birds, KLOMP (1970) concluded that "our knowledge about the heritability of clutch size is negligibly small". Because selection will only result in adaptation if differences between individuals are partly genetic, assumptions on the presence of heritable variation are implicit in the theories on the evolution of clutch size (KLUYVER, 1951; LACK, 1948; 1954).

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In domestic fowl large changes in egg production were obtained by artificial selection (LERNER, 1958). This suggests that heritable variation in egg production traits will also be present in wild birds. However, in contrast to domestic fowl, wild birds produce eggs in definite clutches. Variation in clutch size implies variation in the properties which cause cessation of laying when the characteristic clutch size is reached. In several species further production is then still possible as is revealed by experimental removal of eggs before the clutch is completed (see KLOMP, 1970).

Clutch size is a quantitative trait in which many genes will be involved and interactions with the environment are complex. The only way of assessing the role of heredity is to express the genetic variation as a proportion of the total variation (the heritability). Such estimates are thus dependent on the amount of environmental variation represented in the data. In animal and plant breeding, and in laboratory experiments, heritability estimates are usually made in rather constant specific environments. Whether genetic variation is of any importance in a population in its natural and varying environment can only be told from heritability estimates made under these conditions. Part of the debate on the heritability of IQ in man is based on this methodological point (see e.g. KEMPTHORNE, 1978; LEWONTIN, 1974; 1975). An important purpose of heritability estimates is to predict the potential effect of selection.

Speeds or potential rates of evolution have long been neglected in evolutionary ecology. For instance, in explaining differences between habitats or between mainland and island populations, it makes a great difference whether it takes five or five thousand generations to alter a mean clutch size by a few eggs.

Further, large amounts of genetic variation have been found at the molecular level. It is an open question to what extent this variation has functional significance and is subject to natural selection. The functional significance of enzyme variation is notoriously difficult to investigate. It has only been satisfactorily pursued for few enzyme loci *i.e.* alcoholdehydrogenase and amylase in *Drosophila melanogaster* (see VAN DELDEN *et al.*, 1978 and HOORN & SCHARLOO, 1979), which were used because it was possible to manipulate the substrate concentration in the food medium. The study of genetic variation of characters such as clutch size starts from the other side, namely not from the genetic variation, but from the known ecological importance of the character involved. The ultimate purpose is, of course, to analyse in how far both types of variation can be matched.

Data from the long-term population studies on the Great Tit (*Parus major* L.) where all nestlings were ringed and their parents were identi-



fied, provide a unique source of data for a genetic study. This paper reports an analysis of the data from the four populations studied at the Institute for Ecological Research at Arnhem (KLUYVER, 1951; VAN BALEN, 1973; 1980).

First we will discuss the annual variation in mean clutch size, the effect of female age and the systematic effects of temporal and spatial variation in environmental conditions. We will show that genetic variation for clutch size is present, and finally we will analyse whether selection for clutch size can be demonstrated.

## METHODS

### *The population study of the Great Tit*

KLUYVER (1951) gave three reasons for his choice of the Great Tit for a long-term population study. It is one of the most abundant insectivorous birds in Dutch woodlands, it breeds almost exclusively in nestboxes (if these are provided in sufficient numbers), and the fact that it is mainly resident, which facilitates the determination of density and of the reproductive rate. Throughout the studies the nestlings were ringed in the nest and both parents were caught and identified while feeding the young in their second week of life.

Basic statistics that were recorded are clutch size, date of first egg laying, number of young hatched, hatching date and number fledged. In addition to these, data on body size and egg size are available for a part of the study. Further details of the methods and a description of the study areas can be found in VAN BALEN (1973).

Data from the following areas were analyzed:

- 1) Liesbos, a mature oakwood near Breda. Data are from 1955-1965 and 1976-1979.
- 2) Oosterhout, a mature oakwood near Arnhem, data from 1955-1979.
- 3) Hoge Veluwe, two parts are distinguished: part A with pine stands and part B with mixed coniferous and deciduous wood on poor sandy soil. Data are from 1955-1979. Experiments in 1962-1964, 1967 and 1968 (KLUYVER, 1971) prevent the use of most clutches in these years in the analysis of selection. Extensive damage to the woods by storms in November 1972 and April 1973 necessitated a partial change and a reorganization of the study area. (Part A was reduced from ca. 165 to ca. 30 ha and part B from ca. 145 to ca. 135 ha).
- 4) Vlieland, an island in the Waddensea with a habitat similar to that on the Hoge Veluwe. There are five wooded areas, each about one kilometer apart, four small ones and one larger area that borders on the

village in the eastern part of the island. All Great Tits on the island are studied. Data are available from 1958-1979. Extensive experiments were undertaken in 1960-1963 and 1967-1968 (see KLUYVER, 1971), while a number of adults were removed from the population during second broods in 1970-1975.

In this paper only first clutches will be considered. The problems caused by clutches that could have been repeat clutches instead of first clutches are treated in the discussion.

#### *Methods of quantitative genetics*

Only the basic methods of quantitative genetics (after FALCONER, 1960) could be used in this study. The aim of these methods is to divide the total or phenotypic variance ( $V_p$ ) into two components, the genetic variance ( $V_g$ ) and the environmental variance ( $V_e$ ). The genetic variance as a proportion of the total variance, the heritability ( $h^2$ ), is used as a measure of the extent of genetic determination of the trait ( $h^2 = V_g/V_p = V_g / [V_g + V_e]$ ).

The resemblance between relatives can be attributed to their sharing of genes, if a few conditions such as random distribution of genotypes over environments are fulfilled. The heritability is calculated from the regression coefficient (which measures the resemblance), by multiplying it with the inverse of the proportion of genes shared. For instance, daughters obtain half their genes from the mother, so the heritability is equal to twice the daughter on mother regression. The standard error of the heritability is the standard error of the regression coefficient multiplied by the same factor.

A first approximation of the heritability can often be obtained from the repeatability, that is from the intra-group correlation between repeated measurements made on the same individual. However in this case it is impossible to separate parts of the environmental variation from the genetic variation. This is formalized in a subdivision of the environmental variance into the general environmental variance ( $V_{eg}$ )—which includes the lasting effect of conditions during growth and life-long stay in the same part of the heterogeneous habitat, and can only be observed in the variance between individuals—and into the special environmental variances ( $V_{es}$ ), which is responsible for the variation of measurements made on the same individual. The repeatability ( $r = (V_g + V_{eg}) / V_p$ ) is equal to the heritability when the general environmental variance is zero.

In data from a variable environment that is possibly also spatially heterogeneous it is likely that not all of the conditions for application of these methods are fulfilled. Parents and offspring may well show a re-

semblance that is caused by sharing a similar environment. There are several ways to eliminate such a resemblance caused by correlated environments from a heritability estimate. By expressing clutch size relative to the annual mean clutch size, a large part of the variation due to differences in conditions between years is eliminated. This is the most important traceable component of the environmental variance.

Further we have compared the resemblance between relatives with the resemblance between individuals that are similar in all respects except that they do not share genes. Such comparisons were made in two different ways. It will be shown that males do not influence the clutch size of their partners. Hence, if we treat clutch size as if it were a property of the male, a resemblance in clutch size of *e.g.* (the mates of) fathers and sons is likely to be caused by a correlated environment. If the resemblance between mothers and daughters is partly caused by sharing genes it should be higher than the resemblance along male lines.

We also made two artificial control groups to eliminate the effect of a shared environment. In a list of *e.g.* daughters and mothers (in chronological order of birth year of the daughters and spatially ordered within years) the regression of daughters on the next mother on the list and separately on the previous mother on the list were calculated. The difference between the regression on the true mother and the average of both control group regressions was used in calculating the heritabilities. The standard error of this heritability is based on the standard error of the difference and is roughly a factor  $\frac{1}{2} \sqrt{6}$  larger than the standard error of the original regression coefficient (VAN NOORDWIJK, unpubl.).

#### VARIATION IN ANNUAL MEAN CLUTCH SIZE

Considerable fluctuations in annual mean clutch size have occurred. Basic statistics for Vlieland and Hoge Veluwe are given in an appendix, together with the full distributions. The distributions are approximately normal, although there is a significant negative skewness in the total distributions for both populations. Clutch size on the Hoge Veluwe is significantly larger than on Vlieland, while the variance is also larger in the Hoge Veluwe. There is no significant correlation between the annual means from Vlieland and the Hoge Veluwe and years with a relatively high variance also do not coincide. In both populations, years with a mean clutch size above or below the median of the annual means definitely occur in groups ( $P < 0.05$ , tested with runs test; SOKAL & ROHLF, 1969). This might partly be a consequence of the presence of genetically determined changes in clutch size. But it also has consequences for the measurement of genetic variation. The

average life span of Great Tits that have reached breeding age is about two years. Some mothers and their daughters lived in a run of years with high means and another group in a period with low means. This will cause a non-genetic resemblance between mothers and daughters. The grouping of years with high or low means implies that situations where the mother and daughter lived in years between which a large difference in mean clutch size exists, are less frequent than expected when the sequence was random. This is an extension of the problem caused by mothers and daughters breeding in the same year. It is circumvented when using values relative to the mean.

There is some evidence indicating that the grouping of years is partly a consequence of changes in genetic composition of the populations. In Figure 1 the mean clutch size is given separately for Hoge Veluwe A

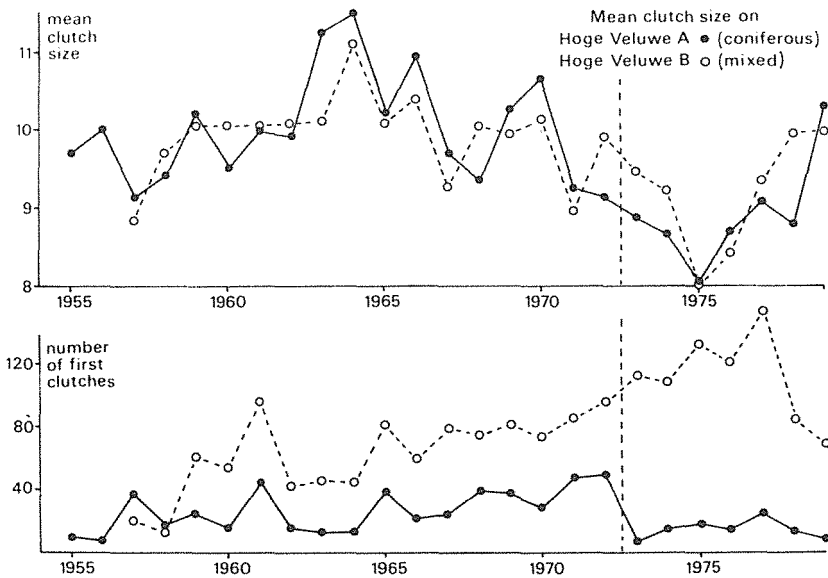


Fig. 1. Mean clutch size and number of first clutches on the Hoge Veluwe A (coniferous) and B (mixed). In 1972/1973 Hoge Veluwe A was reduced to about one quarter of the previous area.

(coniferous) and B (mixed). These two parts are adjacent and many individuals born in one part are breeding in the other. The means of both parts fluctuate in parallel, while there is no consistent difference between the parts. On Vlieland the situation is different. Means for the four small woods and for the area surrounding and including the village are given in Figure 2. There is an uninhabitable stretch, 1.5 km wide

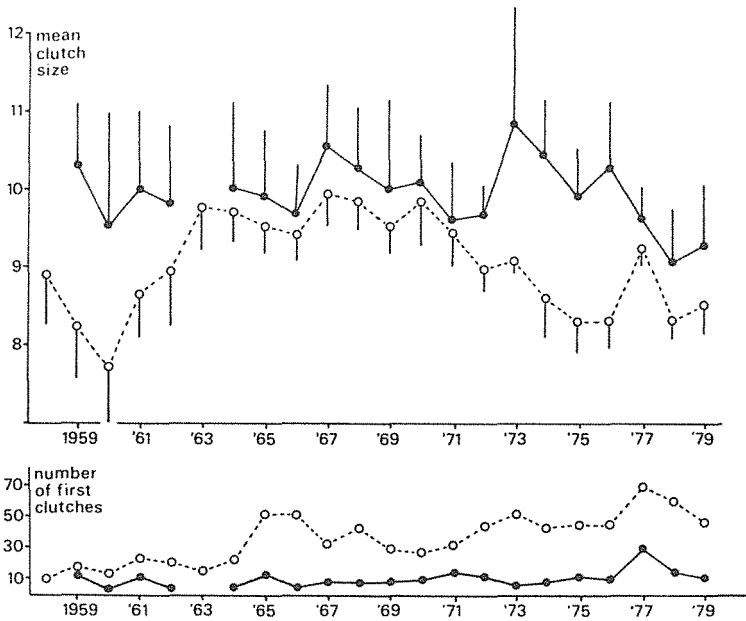


Fig. 2. Mean clutch size and the number of first clutches on Vlieland. —●— four small xxxxx woods, ---○--- main wood and village. Bars represent two standard errors.

between these two parts. The exchange of individuals is only about 10% of that expected if dispersal were random over the whole island (VAN NOORDWIJK, unpubl.). Although several of the smaller fluctuations in the annual mean clutch size are in parallel, the difference between the two parts is large for two runs of years (1959-1961 and 1973-1976) and much smaller in the other years. Differences in habitat between the parts are, in terms of three species, less marked on Vlieland than in Hoge Veluwe. It is unlikely that weather conditions are dissimilar between the parts. Although differences in food situation cannot be excluded, the occurrence and disappearance of a difference in mean clutch size could well be a consequence of genetic drift. If there had been a correlation between mean clutch size in the Hoge Veluwe and Vlieland our interpretation of the possible importance of isolation between subpopulations on Vlieland would have been invalidated.

The number of first clutches also shows a grouping of years with relatively high and low numbers. Throughout the whole study for Vlieland and within the periods 1959-1972 and 1973-1979 for Hoge Veluwe, the number of first broods may be equated with breeding density. In the Hoge Veluwe there is a negative correlation between density and mean clutch size in both periods, but such a correlation is not found on

Vlieland. Moreover, the occurrence of runs in both mean clutch size and density invalidates the assumption of independence of observations in subsequent years. This can largely be avoided by looking at the change in density and the change in mean clutch size from one year to the next. In the Hoge Veluwe this results in lower but still negative correlations, but for Vlieland we found that an increase in density is accompanied by an increase in mean clutch size (Table 1). These correlations are not statistically significant. It is therefore doubtful whether a causal relation exists between density and mean clutch size.

TABLE I  
The relation between density and mean clutch size.

	<i>Hoge Veluwe</i> 1959-1972	<i>Hoge Veluwe</i> 1973-1979	<i>Vlieland</i> 1958-1979
Average number	99	123	46
$s_N$	30.7	34.1	20.5
Average size	10.04	9.15	9.24
$s_{size}$	0.52	0.71	0.51
$r_{(N, size)}$	-0.61	-0.56	-0.07
$P_{(r = 0)}$	0.02	0.17	0.75
Average $\Delta_N$	5.3	-5.3	2.1
$s_{\Delta_N}$	41.0	48.6	17.2
Average $\Delta_{size}$	-0.036	0.10	-0.024
$s_{\Delta_{size}}$	0.69	0.71	0.49
$r_{(\Delta_N, \Delta_{size})}$	-0.40	-0.26	+0.36
$P_{(r = 0)}$	0.17	0.62	0.11

N is the number of first clutches, size is mean number of eggs in first clutches, s is standard deviation,  $\Delta_N$  is number in year (t) — number in year (t-1),  $\Delta_{size}$  is size in year (t) — size in year (t-1).

PATTERNS IN NON-GENETIC VARIANCE

Studying patterns in non-genetic variation is a prerequisite for the study of interaction between genes and environment. Because we want to allow for the effect of genetic differences these analyses will, whenever possible, be made by comparisons within individuals. In the following sections we will analyse the effect on clutch size, of age, of the temporal and of the spatial heterogeneity in the Hoge Veluwe and Vlieland populations.



*The effect of female age*

KLUYVER (1951) showed that yearling females (*i.e.* one year old) have smaller clutches than older females. The difference of about 0.6 egg was apparent in 8 out of 9 years. Several other studies gave similar results (see VAN BALEN, 1973). These differences were found by calculating mean clutch size for different age groups. If a part of the variation in clutch size is genetic such a difference between age groups could not only arise when females tend to increase their clutch size with age, but also if the genetic composition of the age groups is different. Further, a difference in mean clutch size found between age groups may be the result of fluctuations in age composition that are correlated with environmental conditions. VAN BALEN (1973) reported an inconsistent pattern, varying between areas and between 2, 3 and 4 year old females. Such inconsistencies would be expected from the second and third explanation rather than from the first. The question whether females tend to increase the clutch size with age can be studied more directly by comparing the clutch size of a female when it is one year old to its clutch size when it is two years old, etc. The difference in clutch size from one to two years old can be compared with the difference for older age classes. In Figure 3 this is shown for the data from Hoge Veluwe and Vlieland. If the differences are summed over all years the mean difference on Vlieland is  $-0.076$  egg from one to two years old and  $-0.013$  egg for older age groups (not significantly different from 0 or from each other). For the Hoge Veluwe population the values are  $+0.45$  and  $+0.15$  egg respectively in the data from 1966/67 onwards. In the earlier years the differences are  $+0.65$  for one to two years old and  $-0.29$  for older age groups, this difference is significant.

In both populations the proportion of second year survivors (from one to two years old) is variable. In comparing the age difference in each pair of years, increases and decreases in clutch size are found simultaneously in both age groups (Fig. 3). The difference between second year and older survivors in mean change in clutch size on the Hoge Veluwe is mainly due to a higher proportion of second year survivors that lay 3 or 4 eggs more in their second year. For the majority of females the difference in clutch size between one and two years old is not distinguishable from the difference between two and three years old.

These facts suggest that differences in the proportion of young birds in years with a high and with a low mean clutch size play a large role in the average difference in clutch size with age. It implies that testing the hypothesis that females with larger clutches have a higher survival rate should not be done on combined data over several years. The numbers in single years are insufficient to accept or reject the hypothesis of differential survival.

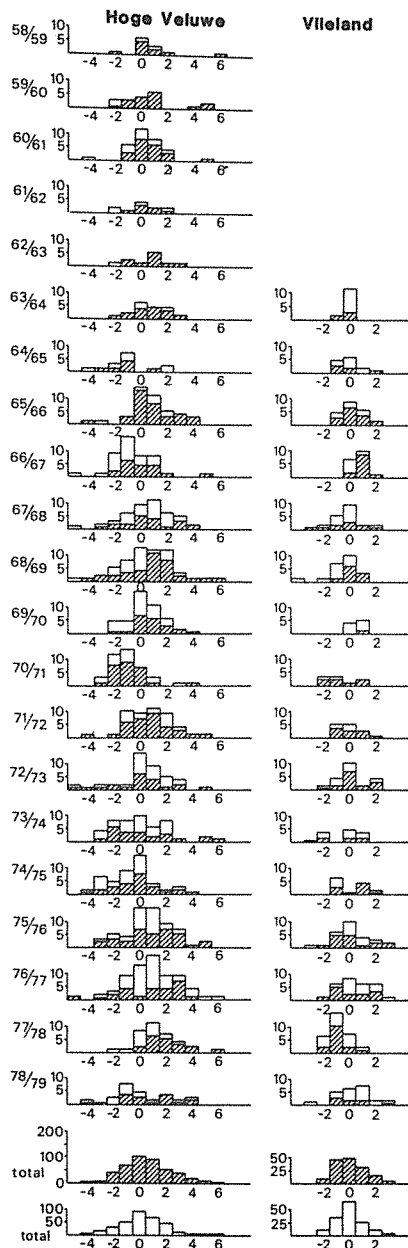


Fig. 3. The difference in clutch size of individual females in producing first clutches in two years. The group that is one year old in the first of these years is indicated by hatching. Left side Hoge Veluwe, on the right Vlieland.

*Temporal variation*

It is evident from Figure 3 that in some pairs of subsequent years most females increase their clutch size and in other years decrease it. In Table 2 the product-moment correlations are given of the clutch size in one

TABLE 2

Correlations between clutch sizes of the same female in two subsequent years.

Years	<i>Vlieland</i>				<i>Hoge Veluwe</i>			
	n	r	mean first year	mean second year	n	r	mean first year	mean second year
58-59					11	0.493	9.8	10.6
59-60	5	0.877	8.0	8.0	19	-0.102	10.0	10.5
60-61	5	0.691	7.8	9.8	32	0.587	10.1	10.7
61-62	7	0.572	9.9	9.4	11	0.739	10.2	10.3
62-63	9	0.686	9.4	9.7	11	0.313	9.9	10.5
63-64	14	0.954	9.9	9.7	18	0.654	10.7	11.3
64-65	14	0.753	9.7	9.6	15	0.365	11.3	10.3
65-66	22	0.642	9.6	9.8	42	0.423	10.0	10.8
66-67	18	0.866	9.7	10.3	43	0.622	10.4	9.6
67-68	23	0.488	10.2	9.9	45	0.260	9.4	9.9
68-69	22	0.418	10.3	9.8	60	0.017	9.8	10.2
69-70	9	0.746	9.9	10.4	45	0.503	10.0	10.4
70-71	9	0.436	9.9	9.1	39	0.655	10.3	9.2
71-72	14	0.586	9.4	9.4	46	0.407	9.2	9.9
72-73	23	0.330	9.1	9.2	41	0.318	9.8	10.1
73-74	14	0.531	9.9	9.4	47	0.246	9.7	9.8
74-75	15	0.639	8.3	8.4	48	0.296	9.0	8.3
75-76	27	0.402	8.3	8.5	57	0.399	7.9	8.5
76-77	28	0.556	8.7	9.2	70	0.393	8.5	9.5
77-78	30	0.712	9.5	8.6	35	0.465	9.1	10.5
78-79	23	0.469	8.7	9.1	30	0.145	9.9	10.0
	$\bar{r} =$	0.586			$\bar{r} =$	0.372		

year with the clutch size of the same female in the next year. There is clearly a relation between the value for the correlation and the width of (variance in) the distribution of differences in clutch size within females. A low correlation is found when the distribution has a high variance. Especially the proportion of individuals with a difference in clutch size of four eggs or more has a large effect on the correlation. These correlations will be further discussed together with the repeatability estimates.

*Spatial variation*

Females show a constancy in performance. It is possible that differences between breeding sites cause differences in clutch size. Because we want to separate the effect of sites from the effect of females, every female should only be counted once in each nestbox. For every nestbox we counted the number of females with a clutch size above or below the mean clutch size in that year. When there are no systematic differences between nestboxes the expectation is roughly a binomial distribution with  $P = 0.5$ . Due to the discrete nature of clutch size the mean is in some years just below or just above a class that contains up to 30% of all observations. Hence, one may expect the variance to be slightly higher than in a binomial distribution. The actual distributions for Vlieland and for two periods on the Hoge Veluwe (due to the total reorganisation in 1972-1973) are given in Figure 4. It can be seen that, on the whole, there is no consistent asymmetry and thus little evidence for site-preference.

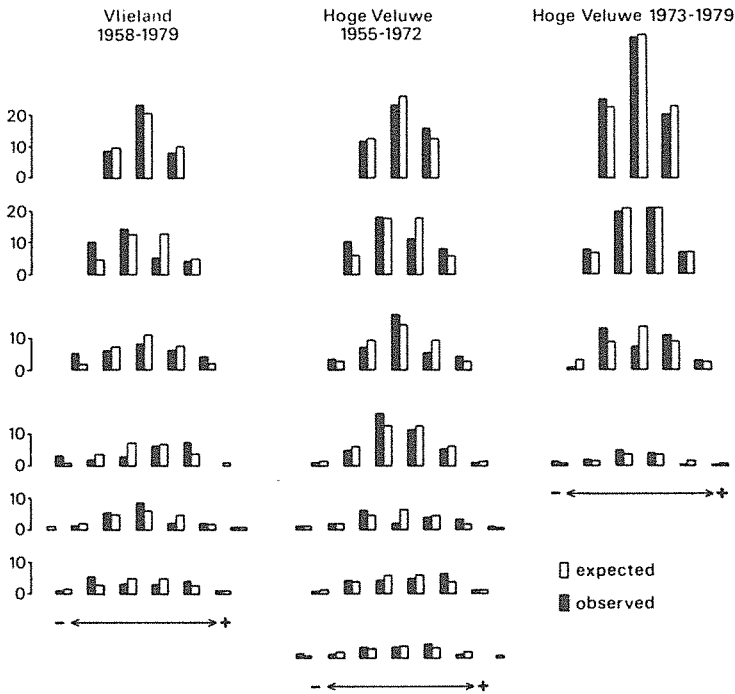


Fig. 4. Number of females in a nestbox with below or above average clutch size, compared to binomial distributions with  $P = 0.5$ . See table 3.

We have tested whether more observations occur in the tails of the distribution than expected. Tails were defined such that both tails together and the centre had expectations as close to 50% as possible (see Table 3). The results are given in Table 4. In each of the three series there is an insignificant tendency towards fewer points in the centre than expected. Given the approximate nature of the P-value of 0.5 the observed deviations from the model show that on the Hoge Veluwe there is no evidence for spatial heterogeneity. On Vlieland some heterogeneity is present, which is probably to a large extent caused by the subdivision of the population.

TABLE 3

The way in which centre and tails of the binomial distribution are defined in Table 4.

number of females													expected frequencies	
													tail	centre
1	1 1													
2	1 2 1												1/2	1/2
3	1 3 3 1												1/4	3/4
4	1 4 6 4 1												5/8	3/8
5	1 5 10 10 5 1												3/8	5/8
6	1 6 15 20 15 6 1												11/16	5/16
7	1 7 21 35 35 21 7 1												29/64	35/64
8	1 8 28 56 70 56 28 8 1												37/128	91/128
9	1 9 36 84 126 126 84 36 9 1												130/256	126/256
10	1 10 45 120 210 252 210 120 45 10 1												176/512	336/512
11	1 11 55 165 330 462 462 330 165 55 11 1												562/1024	462/1024
12	1	12	66	220	495	<b>792</b>	<b>924</b>	<b>792</b>	495	220	66	12	397/1024	627/1024
	tail			centre						tail				

## GENETIC VARIATION

### *Repeatability of clutch size*

The repeatability is considered to give an upper limit to the heritability (FALCONER, 1960). It is an upper limit in the sense that any combination of the effect of genes, lasting effect of conditions during growth, or the effects of site tenacity in a heterogeneous environment can be responsible for the constancy in performance of a single individual. The last of these three possibilities can be tested. Males normally occupy the same territory throughout life. Subsequent partners will thus be subjected to the same environment and if the repeatability of females is mainly due to constancy in environment the repeatability of males (that

TABLE 4

Test whether more nestboxes contain a consistently larger or smaller clutch than expected.

number of females	<i>Vlieland</i> 1958-1979		<i>Hoge Veluwe</i> 1955-1972		<i>Hoge Veluwe</i> 1973-1979	
	expect. t c	observ. t c	expect. t c	observ. t c	expect. t c	observ. t c
2	20-20	17-23	25.5-25.5	28-23	44.5-44.5	45-44
3	8.5-25.5	14-20	11.8-35.3	18-29	14.0-42.0	15-41
4	18.1-10.9	21- 8	22.5-13.5	19-17	21.9-13.1	28- 7
5	7.9-13.1	12- 9	14.6-24.4	12-27	4.5- 7.5	3- 9
6	12.4- 5.6	10- 8	13.1- 5.9	17- 2	2.7- 1.3	3- 1
7	7.7- 9.3	11- 6	9.5-11.5	12- 9		
8	1.7- 4.3	3- 3	3.8- 9.2	3-10		
9	2.0- 2.0	1- 3	1.0- 1.0	2- 0		
10	0.4- 0.6	1- 0	1.7- 3.3	1- 4		
11			1.1- 0.9	1- 1		
12			0.4- 0.6	0- 1		
Total	78.7-91.3 Chi <sup>2</sup> <sub>(1)</sub> = 3.01 P = 0.08	90-80	105.0-131.0 Chi <sup>2</sup> <sub>(1)</sub> = 1.01 P = 0.31	113-123	87.6-108.4 Chi <sup>2</sup> <sub>(1)</sub> = 0.84 P = 0.36	94-102

The numbers in the centre (c) and tails (t) of a binomial distribution with  $P = 0.5$  are summed over the distribution with different numbers of females. For definition of c and t see Table 3.

is the correlation between clutches fathered by the same male) with different partners should have a similar value. The values for this repeatability are positive but much lower than the female repeatabilities. Only the male repeatability for absolute clutch size on Vlieland is significantly different from 0 (Table 5). Site tenacity, assortative mating

TABLE 5  
Repeatability of clutch size.

			<i>N</i> <i>ind./cl.</i>	<i>absolute</i> <i>c.s.</i> <i>r</i>	<i>relative</i> <i>c.s.</i> <i>r</i>
Vlieland	♀	tot.	189/509	0.58	0.54
		sp	79/189	0.57	0.44
		dp	106/244	0.56	0.58
	♂	dp	110/254	0.33	0.22 NS
		sp	75/175	0.61	0.58
Hoge Veluwe	♀	tot	480/1277	0.35	0.36
		sp	120/ 259	0.30	0.19 NS
		dp	328/ 778	0.36	0.37
	♂	dp	301/ 707	0.10 NS	0.08 NS
		sp	133/ 288	0.37	0.32
Liesbos	♀	tot	178/422	0.35	0.30
		sp	40/ 81	0.21 NS	0.43
		dp	70/154	0.37	0.41
	♂	dp	77/182	-0.03 NS	-0.13 NS
		sp	39/ 80	0.32	0.56
Oosterhout	♀	tot	62/165	0.34	0.46
		sp	11/ 22	0.39 NS	0.84
		dp	35/ 89	0.34	0.34
	♂	dp	31/ 72	0.10 NS	0.03 NS
		sp	12/ 24	0.01 NS	0.66

All values differ significantly from 0 except those labeled with NS.

tot = total, sp = with the same partner, dp = with different partner, NS = not significantly different from 0 at 5%.

with respect to some character correlated with clutch size in females (*e.g.* bodysize) and a family relation between subsequent partners can all be responsible for a correlation between successive partners of a male. The consistent difference in mean clutch size between parts of Vlieland (Fig. 2) points in the direction of spatial heterogeneity, but as pointed out above, the heterogeneity might result from the relatedness of females.

On Vlieland a known family relation between male and female exists in 47% of all pairs where grandparents of both are known (VAN NOORDWIJK & SCHARLOO, 1980). The effect of spatial heterogeneity can be analyzed in more detail by looking at the repeatabilities in females that were breeding in the same nestbox, and in males of which subsequent partners bred in the same box (Table 6). It seems that the female repeatabilities are slightly higher and the male values slightly lower than the values in Table 5, but the numbers are small. The conclusion, that there is a female constancy that is considerably higher than the constancy due to being in the same environment when laying the clutch, is confirmed.

TABLE 6  
Repeatabilities within one nestbox; clutch size relative to the yearly mean.

	<i>Vlieland</i>		<i>Hoge Veluwe</i>	
	<i>N</i>	<i>r</i>	<i>N</i>	<i>r</i>
Females with different partners	29/ 60	0.72	66/139	0.39
Pairs	53/118	0.54	61/127	0.30
Males with different partners	39/ 85	0.05	76/159	-0.03

The repeatability values are very similar to the mean of the correlations calculated for every pair of years (Table 2). For Liesbos and Oosterhout the average correlations are  $r = 0.33$  and  $r = 0.28$  based on 13 and 6 pairs of years for which data on at least 5 females were available. The average correlations might be expected to be higher because differences in annual means and variances will have the effect of making the repeatability (*i.e.* the intra-group correlation) lower than the corresponding product-moment correlation. That this is not the case implies that in the total set of years over which the repeatabilities were calculated, situations with different and similar environmental circumstances are balanced. This agrees with the fact that the discrepancy between average correlation and repeatability is largest in Oosterhout for which the number of data is lowest.

*Parent-offspring resemblance*

If the constancy in performance of females has a genetic cause one expects daughters to resemble their mother. Again, the opposite is not necessarily true, a resemblance might also be caused by a resemblance in environment when growing up or when laying, if these are similar for mother and daughter. The results of regression of daughter on mother



and son on father (Table 7) are similar to the repeatability values (Table 5). These heritability estimates are based on comparisons of the average clutch size of an individual. One may also compare each clutch size of the offspring with each value of the parent, or combine all offspring of a parent before comparison.

TABLE 7

Heritability of clutch size in four populations, based on offspring-single parent regression. Average clutch size per individual.

	<i>daughter-mother</i>			<i>son-father</i>		
	<i>n</i>	$h^2 \pm se$		<i>n</i>	$h^2 \pm se$	
Vlieland	362	$0.46 \pm 0.13$		400	$0.25 \pm 0.13$	
Hoge Veluwe	336	$0.34 \pm 0.14$		497	$-0.05 \pm 0.12$	
Liesbos	139	$0.25 \pm 0.21$		127	$-0.15 \pm 0.21$	
Oosterhout	57	$0.50 \pm 0.30$		55	$-0.17 \pm 0.24$	

Each of these three methods has some merits. If one female lays a first clutch in several years, clutch sizes are partly independent with respect to the variation caused by environmental factors, but, of course, not with respect to the genetic variation. Similarly the genes of sisters are only partly different and thus in comparing several daughters with one mother the observations are not completely independent. On the other hand one wishes to attach more weight to comparisons based on the mean of several observations. Using comparisons of the mean clutch size of the mother with the mean of each of her daughters is a compromise between the disadvantages of the other two methods. The values are given in Table 8 for the Hoge Veluwe and Vlieland together with heritabilities based on clutch size relative to the mean of that year and the heritabilities that would be obtained if the correction based on comparison with a parental control group had not been applied. There is no consistent pattern in the difference in results between the three methods.

The effect of the correction is to make the heritability estimates in absolute clutch size lower. The difference between the corrected and the corresponding uncorrected values is not found when the relative clutch size is used. This indicates that a considerable part of the father-son resemblance in the uncorrected absolute clutch size must be attributed to the grouping of years with a high or low mean clutch size.

The male resemblance on Vlieland is rather high. This is in part caused by the fact that in several pairs the female partner of the son is related to the female partner of the father, in three mother-son pairs it is

TABLE 8

Comparison of heritability estimates calculated in different ways.

		<i>N</i>	<i>corrected</i>		<i>uncorrected</i>	
			<i>absolute size</i>	<i>relative size</i>	<i>absolute size</i>	<i>relative size</i>
Vlieland						
Mother-daughter	a.c.	1327	0.29	0.33	0.52	0.41
	m/i	362	0.46	0.49	0.62	0.54
	m/o	204	0.46	0.45	0.68	0.50
Father-son						
a.c.	1505	0.07	0.11	0.31	0.16	
m/i	400	0.25	0.29	0.45	0.32	
m/o	204	0.19	0.25	0.42	0.30	
Hoge Veluwe						
Mother-daughter	a.c.	1242	0.34	0.35	0.35	0.22
	m/i	336	0.34	0.36	0.49	0.24
	m/o	236	0.17	0.23	0.42	0.18
Father-son						
a.c.	1453	-0.03	0.00	0.18	0.02	
m/i	497	-0.05	-0.06	0.38	0.03	
m/o	312	0.13	0.06	0.40	0.05	

a.c. = all combinations, every clutch of e.g. the daughter is compared with every clutch of the mother.

m/i = the mean of the offspring is compared with the mean of the parent.

m/o = the mean of the combined offspring is compared with the mean of the parent.

even the same individual. If all males that are related to their female partners with  $F < 0.125$  are excluded, more than half the resemblance disappears.

Using different methods on the same data does not give us independent estimates, the similarity of which might have enhanced confidence in them. It does, however, indicate that the results are not highly dependent on the implicit assumptions which are different between methods. Therefore the conclusion that about 40% of the phenotypic variation in clutch size has a genetic basis is fairly reliable.

#### *Non-chromosomal transmission?*

Besides chromosomal genes that come to expression only in females, a mother-daughter resemblance might also be caused by maternal effects, cytoplasmic genetic factors or a cultural transmission. If chromosomal genes are responsible for the resemblance in clutch size, it is to be expected that granddaughters show an equal resemblance to their ma-

ternal as to their paternal grandmother. Alternatively, if mother-daughter resemblance is caused by a maternal effect on the environment (during growth) one expects only a resemblance with the maternal grandmother. The simple forms of non-genetic transmission are not supported by the data in Table 9. Although the standard errors of the estimates are high, the agreement with heritability estimates based on parent-offspring regression is good.

TABLE 9  
Heritability estimates based on regression of grandchild on grandparent.

	<i>N</i>	<i>Vlieland</i> $h^2 \pm se$	<i>N</i>	<i>Hoge Veluwe</i> $h^2 \pm se$
Granddaughter on grandmother	478	0.56 $\pm$ 0.18	245	0.74 $\pm$ 0.32
Granddaughter on maternal grandmother	222	0.64 $\pm$ 0.26	108	0.89 $\pm$ 0.49
Granddaughter on paternal grandmother	254	0.47 $\pm$ 0.26	137	0.65 $\pm$ 0.40
Grandson on grandfather	522	0.19 $\pm$ 0.19	312	0.02 $\pm$ 0.27
Grandson on maternal grandfather	244	0.28 $\pm$ 0.26	132	-0.03 $\pm$ 0.40
Grandson on paternal grandfather	278	0.08 $\pm$ 0.28	180	0.05 $\pm$ 0.33

Clutch size is expressed relative to the mean clutch of that year.

#### SELECTION

Recruitment into next years breeding population is used as the criterion for selection. In most years the number of fledglings increases with clutch size (Fig. 5, Table 10 and 11), but this is counteracted by a decrease of recruitment per fledgling with increasing clutch size. The products, recruitment per clutch, do not show a consistent pattern. Although the recruitment is half as high on Hoge Veluwe as on Vlieland, the pattern is similar. On the Hoge Veluwe over half the breeding birds are immigrants. Differential emigration with respect to clutch size might distort the results. The similarity of the results from Vlieland and Hoge Veluwe indicates that this is not a serious problem.

An overall assessment of selection can be expressed in the selection differential. This is the difference between the population mean and the mean of the parents that contributed to the next generation (weighted for the number of offspring). The selection differentials (Table 12 and 13) agree with the regression coefficients of the numbers recruited per clutch on clutch size in Table 10 and 11 (for Vlieland  $r_s = 0.85$ ,  $n = 12$ ,  $P < 0.01$ ; for Hoge Veluwe  $r_s = 0.49$ ,  $n = 15$ ,  $P = 0.06$ ). This indicates that the linear regression gives a reasonable approximation of the end product of many processes, most of which are undoubtedly not linear.

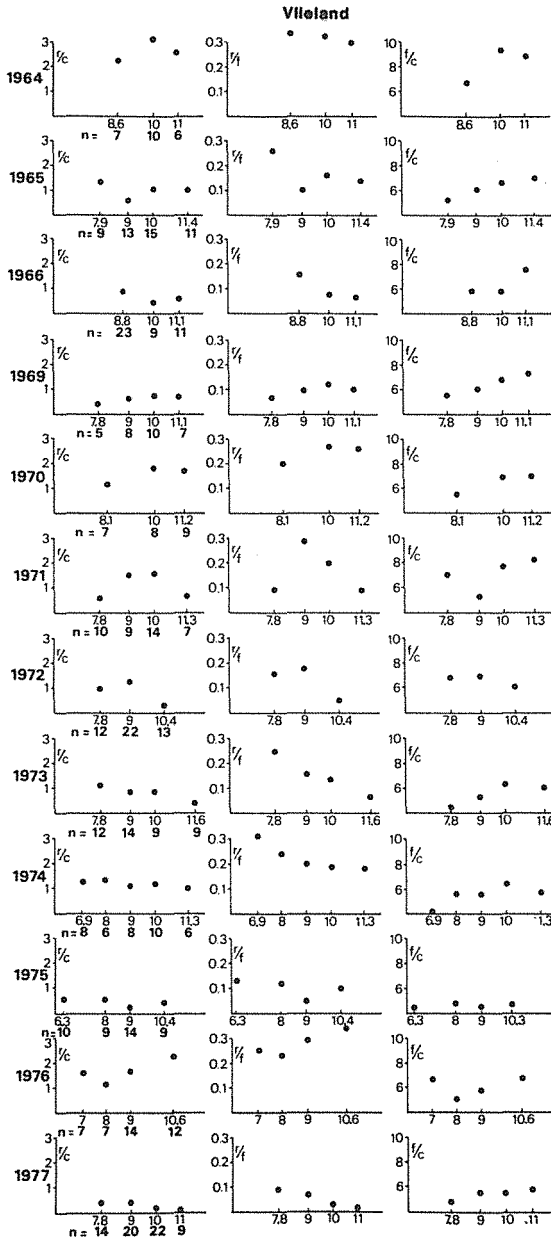


Fig. 5. Numbers recruited per clutch ( $r/c$ ), recruited per fledgling ( $r/l$ ) and fledged per clutch ( $f/c$ ) as functions of clutch size. Clutches where parents were known to be related, and clutches that were manipulated were excluded. Data from Vlieland.

TABLE 10  
Recruitment as a function of clutch size on Vlieland.

Year	N	R/F		F/C		R/C	
		r	slope	r	slope	r	slope
64	3	-0.93	-0.016	0.83	0.937	0.56	0.185
65	4	-0.56	-0.026	0.98	0.504	-0.24	-0.047
66	3	-0.92	-0.040	0.85	0.758	-0.75	-0.160
69	4	+0.70	+0.010	0.99	0.536	0.84	0.102
70	3	+0.86	+0.021	0.93	0.405	0.87	0.223
71	4	-0.12	-0.008	0.58	0.524	0.06	0.023
72	3	-0.81	-0.044	-0.41	-0.145	-0.73	-0.261
73	4	-0.98	-0.045	0.86	0.467	-0.94	-0.158
74	5	-0.91	-0.028	0.70	0.362	-0.81	-0.059
75	4	-0.55	-0.011	0.30	0.025	-0.58	-0.059
76	4	+0.91	+0.029	0.40	0.191	0.77	0.230
77	4	-0.98	-0.024	0.96	0.299	-0.95	-0.110
x =			-0.0151		0.405		-0.0076
s.d. =			0.0246		0.295		0.161
s.e. =			0.0071		0.0852		0.0466
t =			2.13		4.75		0.16
			P = 0.059		P = 0.0008		P = 0.88
$\text{Chi}^2_{(24)} = -2 \sum \ln P_{(r=0)} = 35.19$							
$P = 0.066$							

Correlations (r) and slope of regressions of recruitment per fledgling (R/F), number of fledglings per clutch (F/C), and recruitment per clutch (R/C) on clutch size.

Although there seems to be selection in some years, the deviation from random recruitment with respect to clutch size is in most years not significant, while the combined probability of these tests is 7% for Vlieland and 17% for the Hoge Veluwe. If we combine the data from both populations the result is just significant ( $\text{Chi}^2_{(54)} = 72.41$ ,  $P = 0.048$ ) If there is selection, it is not in one direction, but rather in opposing directions in different years, while it is in favour of intermediate phenotypes in only a few years.

It can hardly be expected that a response to selection is measurable in these data. The numbers are small, the male contribution is not measurable, and the selection differentials are not very large. Further, the effect on clutch size of environmental differences between years is often larger than the expected response, *i.e.* the product of selection differential and heritability. For the data from Vlieland from 1969 onwards Figure 6 gives the cumulative selection differential (a) and the cumulative difference in annual mean clutch size (d). However, the contribution to

TABLE 11  
 Recruitment as function as function of clutch size on Hoge Veluwe.

	<i>N</i>	<i>R/F</i>		<i>F/C</i>		<i>R/C</i>	
		<i>r</i>	<i>slope</i>	<i>r</i>	<i>slope</i>	<i>r</i>	<i>slope</i>
1958	4	-0.53	-0.030	0.52	0.42	-0.72	-0.110
1959	5	-0.82	-0.009	0.90	0.83	-0.46	-0.020
1960	5	-0.97	-0.020	0.94	1.41	0.79	0.180
1961	7	-0.55	-0.010	0.92	0.68	-0.25	-0.012
1965	5	-0.28	-0.001	0.95	0.89	0.68	0.023
1966	5	-0.30	-0.006	0.79	0.43	-0.06	-0.011
1969	5	-0.47	-0.005	0.94	0.64	0.12	0.007
1970	6	-0.78	-0.013	0.96	0.83	0.54	0.064
1971	5	-0.82	-0.014	0.95	0.93	0.23	0.017
1972	4	-0.70	-0.016	0.91	0.57	-0.31	-0.019
1973	6	-0.07	-0.001	0.80	0.31	0.32	0.026
1974	3	+0.98	0.015	-0.18	-0.06	0.74	0.070
1975	6	+0.07	0.0006	0.91	0.37	0.34	0.013
1976	6	+0.05	0.0007	0.74	0.55	0.69	0.088
1977	7	-0.47	-0.0006	0.93	0.73	0.08	0.006
$\bar{x}$ =			0.0076		0.636		0.0215
s.d.			0.0105		0.338		0.0639
s.e.			0.0027		0.087		0.165
t			2.81		7.31		1.30
			$P = 0.015$		$P = 6 \times 10^{-6}$		$P = 0.22$
					$\text{Chi}^2_{(30)}$		$= 2\sum \ln P_{(r=0)} = 37.23$
							$P = 0.17$

Correlations (*r*) and slope of regressions of recruitment per fledgling (*R/F*), number of fledglings per clutch (*F/C*), and recruitment per clutch (*R/C*) on clutch size.

the population differs greatly from year to year, therefore the selection differential was weighted by the number of recruits/number of clutches (b). In order to eliminate the effect of annual differences in environmental conditions we corrected the difference between the annual means with the mean difference in clutch size (c) of all individuals that bred in both years, taken from Table 2. The curves (b and c) do show some resemblance especially if one takes the selection differential in previous years into consideration, which gives an indication of the expected male contribution. For this reason the fact the resemblance is better in the last few years is to be expected.

DISCUSSION

We have made an analysis of the number of eggs in the completed first clutch. Although females laying a large first clutch also tend to have a

TABLE 12  
Selection differentials on Vlieland

<i>Year</i>	<i>n</i> <i>clutches</i>	<i>n</i> <i>recruits</i>	<i>mean of</i> <i>base pop.</i>	<i>mean</i> <i>of parents</i>	<i>weighted</i> <i>sel. diff.</i>
1964	28	71	9.79	9.83	+0.04
1965	58	54	9.67	9.56	-0.11
1966	55	39	9.51	9.28	-0.23
1969	38	22	9.63	9.86	+0.23
1970	26	40	9.92	10.05	+0.13
1971	45	58	9.51	9.71	+0.20
1972	55	51	9.07	8.86	-0.21
1973	52	43	9.31	9.02	-0.29
1974	46	54	8.98	8.93	-0.05
1975	52	24	8.56	8.47	-0.09
1976	48	86	8.79	8.97	+0.18
1977	86	31	9.37	9.02	-0.35

relatively large second clutch (VAN NOORDWIJK, unpubl.), clutch size in second and repeat broods is influenced by more factors than the size of first clutches. Total egg production would be strongly influenced by the frequency of second clutches. Further, the recruitment from second and repeat clutches is, at least locally, much lower than that from first clutches (DHONDT & HUBLÉ, 1968).

TABLE 13  
Selection differentials on Hoge Veluwe.

<i>Year</i>	<i>n</i> <i>clutches</i>	<i>n</i> <i>recruits</i>	<i>mean of</i> <i>base pop.</i>	<i>mean</i> <i>of parents</i>	<i>weighted</i> <i>sel. diff.</i>
1958	29	28	9.59	9.46	-0.13
1959	78	21	10.15	9.90	-0.25
1960	40	67	9.88	10.66	0.18
1961	117	10	9.97	9.50	-0.47
1964	24	29	11.13	11.48	0.35
1965	116	28	10.05	10.54	0.49
1966	78	64	10.45	10.53	0.08
1969	99	52	9.99	10.13	0.14
1970	89	118	10.22	10.33	0.11
1971	65	38	9.09	9.26	0.15
1972	84	21	9.42	9.24	-0.16
1973	64	21	9.23	9.29	0.06
1974	57	39	9.19	9.23	0.04
1975	138	31	8.02	8.00	-0.02
1976	114	83	8.42	8.52	0.10
1977	145	43	9.37	9.58	0.21

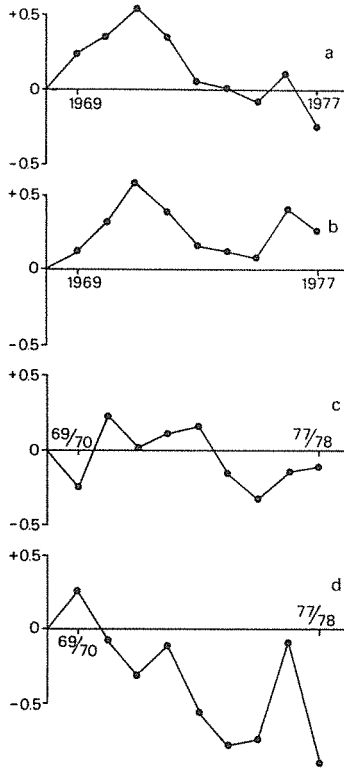


Fig. 6. Response to selection on Vlieland 1969-1977. a) Cumulative selection differential, b) cumulative selection differential weighted by number of recruits/number of first clutches, c) cumulative difference in population mean corrected for year effects by adding the mean intra-individual difference for each pair of years. The difference in the following year is shown in corresponding position. d) uncorrected cumulative difference in population mean.

There are a number of clutches for which it is impossible to decide whether they are late first clutches or repeat clutches where the corresponding first clutch is not known as such. There is reason to suspect that most of the extreme differences between clutch sizes (Fig. 3 and Fig. 4) of the same female belong to this category. Especially on the Hoge Veluwe there are far more extreme differences than expected from the variance of the distributions. In many cases there is no independent criterion to discriminate between the first clutch of a late female and the repeat clutch of an early female. We have regarded every clutch as a first clutch unless either the male or the female was known to have had an earlier clutch, or unless it was started more than



30 days after the first clutch in the population in that year. It is not unlikely that the difference between the heritability estimates for the Hoge Veluwe and Vlieland is caused by a higher proportion of clutches that were in fact repeat clutches on the Hoge Veluwe.

It is self-evident that the occurrence of such events with a low frequency ( a few percent) but with a large effect (on the covariance) necessitates the use of a large number of observations, while only a long period of study can ensure a representative sample of environments. Previous studies in which repeatability or heritability of clutch size was demonstrated (see KLOMP, 1970 for ref.) were based on much smaller samples; shorter periods and, although the possibility of resemblance through correlated environments was recognized (*e.g.* KLUYVER, 1951), it was not analyzed. KLUYVER (1951) gave data on 104 females from which a repeatability of 0.28 can be calculated. He attributed the fact that in some boxes clutches are early, while in others they are consistently late, to occupation by the same early or late females in subsequent years. Nevertheless, he concluded that the role of heredity in the determination of clutch size was negligible (KLUYVER, 1963). The study of the Wytham data on the Great Tit by Jones (JONES 1973; PERRINS & JONES, 1975) had numbers comparable to our data from Liesbos. Although their use of several corrections might be misleading (see below), their estimate of  $h^2 = 0.48$  and a repeatability of 0.51 is in the same range as our estimates.

VAN BALEN *et al.* (in prep.) studied the breeding biology of the Great Tit in natural holes near Arnhem. Preliminary results indicate that there is no difference in clutch size between nestboxes and natural holes. Their results further indicate that there is no simple relation between clutch size and size of the hole, in contrast to what has been reported for nestboxes of different size (KARLSSON & NILSSON, 1977). If nesting holes of different quality are available, it is conceivable that the birds with larger clutches are found in the "better" holes (*cf.* MOEED & DAWSON, 1979). In a study with standard-size nestboxes, this potential complication is not present.

The use of corrections introduces more problems than are resolved. For example in his study of the heritability of clutch size in the Great Tit, JONES (1973) added the mean difference for age, the mean difference for the particular year and the mean difference of the area. However, population size is not constant, and in years with high density the proportion (and number) of first-year birds is high. Thus an average effect of age and an average effect of density measure partly the same difference in mean clutch size. If females that produce large clutches have a higher survival rate (both might be caused by a better ability to procure food) a difference between the mean clutch size of first-year and

older birds will be the result, even without any effect of age in individual birds. Many similar complications in the use of corrections might arise, but it is impossible to examine all of them.

Further, there is also a logical argument against the use of corrections for known environmental causes of variation. If one were to succeed in eliminating all environmental variance, then by definition only genetic variance would be present and the heritability would be 1.0. This suggests that a heritability based on values corrected for known systematic sources of environmental variance might be used to test what proportion of environmental variance can be accounted for, but the information content with respect to the importance of genetic variation is lost. In general the only environmental variance that may be eliminated from a heritability estimate is the part that is irrelevant to the selection applied, or measured. Because selection will operate within year classes, elimination of between-year variation in clutch size does not affect the use of the heritability estimate in evaluating the effect of selection on the population mean.

Our main conclusion is that about 40 percent of the phenotypic variation in clutch size is genetic. This implies that directional selection will result in rapid changes in mean clutch size. There are, however, a number of problems associated with the use of the methods of quantitative genetics (see *e.g.* LEWONTIN, 1974).

Further, an important problem is formed by the correlation of environments in which relatives live. In general an analysis of parent-offspring resemblance is less sensitive to this problem than an analysis of the resemblance between sibs. The number of sister pairs in our data is too small to be of any use. There is, on the whole, little reason to suspect that in our heritability estimates an important role is played by correlated environments. This is supported by a reasonable agreement between the repeatability of females, the heritability based on daughter-mother regression and the heritability based on granddaughter-grandmother regression. And further, there are three independent ways in which the possible effects of correlated environments could be investigated, 1) by comparing phenotypes along male lines, 2) by using artificial control groups and 3) by using clutch size relative to the annual mean. Although there are several subtle differences between these methods, the results are very similar, indicating that apart from variation between years no important systematic factors influencing clutch size are present in the data studied.

The selection for clutch size, although barely significant, is similar to that found in the Wytham study (based on recaptures after at least three months). In most years either the largest or smallest clutches are most productive, the intermediate ones are rarely so (LACK, 1966). In

many years nestling weight is negatively correlated with brood size, as is the number of feeds per nestling (PERRINS, 1965; VAN BALEN, 1973), while the proportion recaptured after at least three months decreases with fledgling weight. This is in agreement with our findings that in almost any year the number of recruits per fledgling is negatively correlated with clutch size. There is a potential complication in the use of weight as a measure of condition, because 60% of the variation in adult average body weight is genetic (VAN NOORDWIJK *et al.*, in prep.). There are some indications that the difference between the average value of the nestlings and the midparent value for weight gives a better indication for the conditional aspects of weight. In the data for the Hoge Veluwe, where weights are known for about 70 percent of all females recorded breeding, there is, surprisingly, no correlation between weight and clutch size (VAN NOORDWIJK, unpubl.). Equally surprising is that clutch size and egg volume are also not correlated, although a major proportion (some 60-80%) of the phenotypic variation in egg volume is genetic (VAN NOORDWIJK *et al.*, 1981).

Having demonstrated that a considerable amount of genetic variation is present in natural populations of the Great Tit, the question arises how it is maintained. At present this question can not be answered, likewise there are still many obscure points in the interrelationships of several traits with ecological importance.

It seems beyond doubt that directional selection would result in rapid changes in population mean. The potential rates of change that can be calculated from the heritability estimates suggest that differences of a few eggs in clutch size can be brought about in a matter of decades. Such a difference is similar to the largest differences in clutch size observed between tit species. One of the nest questions is going to be: Why has so little evolutionary change actually taken place, while the potential for rapid change is so large?

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## APPENDIX 1

Basic statistics for first clutches with clutch size 5-15.

<i>Hoge Veluwe</i>	<i>Year</i>	<i>N</i>	<i>mean</i>	<i>var.</i>	<i>st. dev.</i>	<i>st. err.</i>	<i>C.V.</i>	<i>g1</i>	<i>g2</i>
	55	10	9.70	2.68	1.64	0.52	16.87	0.03	-0.92
	56	8	10.00	2.00	1.41	0.50	14.14	-0.32	-0.96
	57	57	9.02	2.80	1.67	0.22	18.57	-0.12	-0.52
	58	31	9.55	1.86	1.36	0.24	14.27	-0.34	0.66
	59	86	10.12	2.79	1.67	0.18	16.50	-0.75	0.91
	60	72	9.94	2.19	1.48	0.17	14.90	-0.06	-0.06
	61	140	10.04	2.84	1.69	0.14	16.79	-0.19	0.59
	62	57	10.07	2.82	1.68	0.22	16.67	-0.20	0.36
	63	59	10.36	2.47	1.57	0.20	15.19	-0.17	-0.04
	64	59	11.22	3.04	1.74	0.23	15.53	0.09	-0.25
	65	121	10.15	2.68	1.64	0.15	16.12	-0.39	0.33
	66	81	10.54	2.08	1.44	0.16	13.67	-0.45	0.04
	67	103	9.36	2.72	1.65	0.16	17.63	-0.32	0.07
	68	115	9.79	2.62	1.62	0.15	16.54	-0.22	0.22
	69	118	10.04	2.43	1.56	0.14	15.54	-0.79	1.63
	70	93	10.30	2.08	1.44	0.15	14.01	-0.65	-0.18
	71	133	9.05	2.39	1.55	0.13	17.10	-0.17	-0.00
	72	145	9.65	2.99	1.73	0.14	17.93	0.16	0.45
	73	110	9.41	3.18	1.78	0.17	18.95	-0.20	-0.14
	74	113	9.13	3.17	1.78	0.17	19.49	0.02	0.39
	75	150	8.01	2.44	1.56	0.13	19.49	0.45	0.89
	76	127	8.43	2.33	1.53	0.14	18.09	-0.07	-0.31
	77	181	9.31	2.65	1.63	0.12	17.48	-0.29	-0.14
	78	99	9.77	2.67	1.63	0.16	16.73	-0.71	0.59
	79	78	10.01	2.32	1.52	0.17	15.23	0.04	0.09
Total		2346	9.60	3.07	1.75	0.04	18.26	-0.19	0.03

<i>Vlieland</i>	<i>Year</i>	<i>N</i>	<i>mean</i>	<i>var.</i>	<i>st. dev.</i>	<i>st. err.</i>	<i>C.V.</i>	<i>g1</i>	<i>g2</i>
	58	13	9.15	1.31	1.14	0.32	12.49	0.04	0.40
	59	30	9.17	3.18	1.78	0.33	19.45	-0.26	0.08
	60	17	8.12	2.24	1.50	0.36	18.42	-0.09	-0.14
	61	34	9.09	2.26	1.50	0.26	16.56	-0.04	-0.36
	62	25	9.12	2.11	1.45	0.29	15.93	-0.96	0.70
	63	19	9.68	1.56	1.25	0.29	12.90	-0.43	-0.25
	64	28	9.75	0.94	0.97	0.18	9.92	-0.74	0.68
	65	65	9.63	1.49	1.22	0.15	12.66	0.11	-0.10
	66	57	9.44	1.32	1.15	0.15	12.18	-0.20	0.28
	67	43	10.07	1.45	1.20	0.18	11.95	0.36	-0.44
	68	50	9.88	1.29	1.14	0.16	11.50	-0.69	-0.02
	69	38	9.63	1.32	1.15	0.19	11.93	-0.44	-0.10
	70	37	9.89	1.65	1.29	0.21	13.00	-1.54	3.81
	71	47	9.55	1.56	1.25	0.18	13.06	0.01	-0.51
	72	57	9.12	1.00	1.00	0.13	10.98	0.40	0.35
	73	57	9.32	1.79	1.34	0.18	14.37	0.49	0.05
	74	52	8.87	2.59	1.61	0.22	18.15	0.14	-0.92
	75	56	8.64	2.16	1.47	0.20	17.01	-0.40	-0.22
	76	54	8.70	2.02	1.42	0.19	16.34	0.34	0.86
	77	100	9.34	1.10	1.05	0.10	11.21	-0.24	-0.59
	78	75	8.49	1.31	1.14	0.13	13.46	-0.01	-0.25
	79	58	8.64	1.78	1.33	0.18	15.44	0.15	-0.24
Total		1012	9.23	1.83	1.35	0.04	14.65	-0.21	0.09

APPENDIX 2  
Distributions of clutch size.

*Hoge Veluwe*

<i>year clutch</i>	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	<i>Total</i>
5	0	0	0	0	2	0	1	0	0	0	1	0	3	1	3	0	2	1	3	4	7	4	2	2	0	36
6	0	0	6	1	1	1	3	1	1	0	2	1	2	3	1	0	6	5	3	5	18	8	9	2	0	79
7	1	0	4	2	2	2	7	5	1	0	4		5	3	2	5	12	8	8	8	31	26	15	8	5	164
8	1	2	11	0	9	9	12	4	3	5	10	7	20	17	8	9	25	16	20	17	37	22	23	4	8	299
9	3	0	13	13	10	14	20	5	14	3	22	8	26	24	22	7	37	42	21	37	38	37	46	18	13	493
10	2	3	11	9	25	21	45	18	12	13	20	24	20	26	36	24	27	31	24	21	12	21	44	35	22	556
11	1	2	10	3	19	16	29	18	13	11	26	17	17	28	28	30	20	24	20	11	3	6	29	17	20	418
12	2	1	1	3	16	5	15	2	11	15	21	19	9	8	15	16	2	10	6	5	3	3	10	11	7	216
13	0	0	1	0	1	4	5	2	3	7	3	5	1	4	2	2	2	5	5	4	0	0	3	2	1	62
14	0	0	0	0	1	0	2	2	1	2	2	0	0	1	1	0	0	2	0	1	1	0	0	0	2	18
15	0	0	0	0	0	0	1	0	0	3	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	5
Total	10	8	57	31	86	72	140	57	59	59	121	81	103	115	118	93	133	145	110	113	150	127	181	99	78	2346

*Vlieland*  
*year clutch*

	58	59	60	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	<i>Total</i>	
5	0	1	1	0	1	0	0	0	0	0	0	0	1	0	0	0	0	1	1	0	0	0	6	
6	0	2	1	2	0	0	0	0	1	0	0	0	0	0	0	0	2	5	0	0	3	3	19	
7	1	1	3	2	2	1	1	2	1	0	2	2	0	2	2	4	12	6	11	4	11	8	78	
8	2	5	6	8	5	3	1	10	7	3	4	4	3	8	12	11	8	10	10	18	23	16	177	
9	6	9	3	9	4	2	8	17	24	12	10	9	7	12	26	20	10	17	19	31	25	17	297	
10	2	5	2	7	10	9	12	21	12	14	17	15	13	15	12	12	14	9	34	10	9	266		
11	2	5	1	4	3	3	6	12	11	8	16	7	12	7	4	6	5	2	2	13	3	4	136	
12	0	1	0	2	0	1	0	2	1	5	1	1	1	3	1	3	3	1	1	0	0	1	28	
13	0	1	0	0	0	0	0	1	0	1	0	0	0	0	0	1	0	0	1	0	0	0	5	
Total		13	30	17	34	25	19	28	65	57	43	50	38	37	47	57	57	52	56	54	100	75	58	1012

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