

HERITABILITY OF EGG SIZE, HATCH WEIGHT, BODY WEIGHT, AND VIABILITY IN RED GROUSE (*LAGOPUS LAGOPUS SCOTICUS*)

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ABSTRACT.—Heritabilities of egg size (0.7 ± 0.2), hatch weight (0.5 ± 0.1), chick viability (0.3 ± 0.2), and body weight at 75 days of age (0.6 ± 0.1) are given for Red Grouse (*Lagopus lagopus scoticus*). Much of the variation in mean egg size amongst wild hens within years was due to inherent differences amongst hens and had little to do with differences in their environment. Cocks had no detectable effect on the egg size of their mates or the hatch weight and viability of their chicks, but did affect their chicks' body weight. It seems that egg size in Red Grouse is determined largely by inherited factors and in turn affects hatch weight and viability. Received 23 November 1981, accepted 16 March 1982.

In several species of wild birds, chicks from big eggs survive better until fledging than chicks from small eggs (Schifferli 1973, Davis 1975, Parsons 1975, Lundberg and Väisänen 1979). Most studies have not separated the effects of the hen's intrinsic nature, her environment, and her chicks' environment. In Red Grouse (*Lagopus lagopus scoticus*), however, the survival of newly hatched chicks is related to egg size independently of the chicks' environment (Moss et al. 1981). One can therefore ask: What is the relative importance of heredity and environment in determining egg size?

The "heritability" of a trait is usually defined as the ratio of additive genetic to total phenotypic variance (Falconer 1964). It is assumed that effects that are consistently transmissible from parent to offspring, after environmental effects have been ruled out, are "genetic." This deduction is made not by studying the genes themselves but by statistical inferences from observed patterns of phenotypic variance.

An important reason for calculating heritability is to enable one to predict the potential effect of selection (van Noordwijk et al. 1981a). Estimates of heritability are usually made from data on resemblances between relatives, but resemblances may result not only from the sharing of genes but also from the sharing of environments. For example, if a large well-fed mother has large well-fed offspring, the resemblance between them may be due to the good feeding.

In the present study we ruled out environmental covariance by collecting clutches of eggs from the wild, hatching and rearing chicks from

these eggs in standard conditions (Moss et al. 1981), and measuring the size of eggs laid by these grouse in subsequent years in captivity.

METHODS

Conventional analyses of variance were used to estimate the repeatability of individual measurements within clutches, the repeatability of mean clutch values in successive years, and intraclass correlations between sibs. These gave upper limits of heritability. Regressions of offspring values on parents gave estimates of heritability: this was calculated by dividing the regression coefficient by the degree of kinship. If data came from several years, correlations and regression coefficients were calculated separately for each year and the results combined to give averages weighted in proportion to the number of samples in each year. Standard errors were calculated by pooling the residual mean squares for each year (Sprent 1969).

Egg size (length \times breadth²) was measured as in Moss et al. (1981), who also described the husbandry of the grouse. Our measure of viability was the percentage survival of chicks in a clutch up to 15 days of age in standard aviary conditions (Moss et al. 1981). All measures were regarded as properties of the clutch, so that sibs from eggs laid in the wild had the same parent values but different offspring values. As the data on viability in the present paper were not normally distributed, we have used \log_{10} mortality when calculating the heritability of viability. This had little effect on the estimated heritability but, because \log_{10} mortality was more normally distributed, reduced the variance.

"Hill" eggs were laid by wild hens at Kerloch Moor in Kincardineshire and then taken into the aviary before hatching. "Aviary" eggs were laid in the aviary by birds hatched from hill or aviary eggs. Some

TABLE 1. Repeatability of measurements of individual egg size (length \times breadth²) within clutches.

Year	Hill eggs			Aviary eggs		
	Number of clutches	Number of eggs	Repeatability	Number of clutches	Number of eggs	Repeatability
1971	24	183	0.65	16	80	0.58
1972	25	158	0.62	15	75	0.76
1973	23	146	0.66	15	75	0.57
1974	18	123	0.69	15	75	0.47
1975	19	127	0.58	15	75	0.43
1976	18	122	0.65	15	75	0.69
1977	17	126	0.71			

^a Fifteen or 16 hens in their first year were chosen at random, and, from each of these, five eggs were chosen at random from the available data.

wild hens were marked, and we measured their eggs on the hill in successive years.

RESULTS

Repeatability of egg size within clutches and years.—The mean repeatability of egg size of hill eggs (0.65, Table 1) only slightly exceeded that for aviary eggs (0.58, difference NS). As the aviary environment was similar for all hens, variations in it presumably had little effect on differences in egg size amongst hens. If so, it seems that variations in the wild environment also had relatively little effect on variations in egg size and that much of the observed variation was due to intrinsic differences amongst hens (up to 0.6) and much to developmental or random variation within hens (up to 0.4).

Repeatability of mean egg size within individuals between years.—Despite small samples, this was very similar for eggs laid in successive years, both by the same marked hens in the wild and by hens in captivity (Table 2). Pooling the data from hill and aviary eggs suggested that hens in their second year laid larger eggs than those they had laid in their first year (1.27 ± 0.043 units, equivalent to 0.6 g, $P < 0.01$, paired t -test). It was not clear whether this was an effect of age or of a difference between years. Despite this source of error, which would reduce repeatability, some 0.7–0.8 of the total variance was attributable to differences amongst hens.

Heritability of egg size.—Sisters hatched in the aviary from the same clutch of hill eggs tended to lay eggs of the same mean size (Table 3), and daughters' eggs resembled mothers'. The most precise estimate of heritability (0.66 ± 0.14) came from the regression of aviary daughters on hill mothers.

The estimate of heritability at 0.66 was almost identical with that of repeatability (0.65 for hill, 0.58 for aviary eggs). In theory, repeatability comprises heritability and "general environmental variance," i.e. effects of the environment on the mean size of the eggs in a clutch. Such variance seems to be very small in these data, confirming that differences in the environment of wild hens had little effect on the relative size of their eggs. This conclusion is similar to that of van Noordwijk et al. (1980) for Great Tits (*Parus major*).

Heritability of other traits.—Heritability of body weight at 75 days of age was similar to that of egg size (Table 4). In this case a father/son estimate was possible; father/son heritabilities are usually thought to be entirely genetic in origin, because the possibility of non-genetic maternal effects is ruled out. As father/son and mother/daughter estimates were similar, such maternal effects probably did not inflate the mother/daughter estimates of this parameter.

Hatch weight is determined partly by egg size but also the the loss in weight between laying and hatching (Moss et al. 1981). Whilst the fathers' genes do not affect egg size directly, they might affect the loss in weight. How-

TABLE 2. Repeatability of mean egg size for the same individuals in successive years.

	Hill eggs ^a	Aviary eggs ^b
Number of hens	9	13
Repeatability	0.73	0.77
Significance level	0.01	0.001

^a Hens, hatched in year i (4 in 1963, 1 in 1968, 4 in 1969), laying in years $i + 1$ and $i + 2$.

^b Hens hatched in 1970, laying in 1971 and 1972.

TABLE 3. Heritability of mean egg size.

	Number of pairs	Correlation or regression coefficient ± SE	Degree of kinship	Heritability ^a
Correlation between aviary sisters from the same hill clutch	24	0.55 ± 0.29	0.5	1.1 ± 0.6
Regression of aviary daughters on aviary mothers	28	0.61 ± 0.20	0.5	1.2 ± 0.4
Regression of aviary daughters on hill mothers	111	0.33 ± 0.07	0.5	0.66 ± 0.14

^a Theoretical maximum 1.0.

ever, there was no significant effect of fathers on hatch weight (Table 4). The heritability of hatch weight from mother to offspring may therefore be a result of the inheritance of egg size.

Hatch weight is correlated with the viability of chicks in standard conditions in captivity (Moss et al. 1981). Although viability was transmitted from mother to daughter, the fathers again had no detectable effect, as with hatch weight. These data are consistent with the idea that egg size is genetically determined, that egg size is a determinant of hatch weight, and that hatch weight affects viability. There is no evidence of a direct genetic (paternal) effect on hatch weight or viability.

DISCUSSION

Much of the variation in egg size amongst wild Red Grouse within years was due to inherent differences amongst hens and had little to do with differences in their environment. Certainly, environment can affect egg size

(Sharp and Moss 1981), but it seems to have been relatively unimportant at Kerloch Moor within years from 1971 to 1977.

It has been argued that traits of importance to genetic fitness should have a low heritability (Falconer 1964). The reasoning is that there is likely to be an optimum value for each trait, which would become fixed at this optimum by natural selection. There is little doubt, however, that egg size contributes to fitness in wild birds, and yet it is highly heritable, at least in Great Tits, Pied Flycatchers (*Ficedula hypoleuca*) (Jones 1973, Ojanen et al 1979, van Noordwijk et al. 1980), and Red Grouse. A possible explanation is that, although egg size is correlated with the number of chicks reared per clutch in wild birds, its effect on chick production may be small compared with other effects. The heritability of chick viability is low, and this, rather than egg size *per se*, is likely to be important for fitness. Alternatively, different egg sizes may be the fittest in different years, as has been shown for clutch size and

TABLE 4. Heritability of hatch weight, body weight at 75 days of age, and viability.

		Heritability ± SE	Degrees of freedom	Significance level
Hatch weight	Mother-daughter	0.45 ± 0.13	97	0.001
	Father-daughter	-0.20 ± 0.20	88	NS
Body weight ^a	Mother-daughter	0.58 ± 0.24	75	0.001
	Father-daughter	0.52 ± 0.22	75	0.025
	Father-son	0.50 ± 0.20	76	0.025
	Mother-son	0.43 ± 0.27	75	NS
	Midparent-midoffspring ^b	0.65 ± 0.13	65	0.001
Viability	Mother-daughter	0.30 ± 0.16	77	0.05
	Father-daughter	-0.22 ± 0.19	77	NS

^a Mother-father correlation for body weight 0.04 (NS).

^b Mean of mean sons and mean daughters.

laying date in Great Tits by van Noordwijk et al. (1980). If so, this would maintain genetic variability.

As pointed out by van Noordwijk et al. (1981b), a high heritability of egg size implies a potentially rapid response to selection. Egg size in Red Grouse varied between years at Kerloch (Jenkins et al. 1967), and the possibility that such changes were a result of genetic selection, rather than an effect of environmental variation, cannot be ruled out.

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