

AN ABSTRACT OF THE THESIS OF

Lavinia A. Hales for the degree of Master of Science in Poultry Science presented on July 24, 1987.

Title: Heritability Estimates for Semen Volume
in Medium White Turkeys

Redacted for Privacy

Abstract Approved: _____

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A population of Wrolstad strain Medium White turkeys has been divergently selected for low and high mean semen volume for 13 generations. A mean volume difference of .34 mls. was obtained in the 13th generation; with the low line averaging .21 mls. and the high .55 mls. Heritability estimates determined by the full sib correlation method averaged $.61 \pm .13$ and $.54 \pm .15$ for the low and high lines, respectively. Realized heritabilities for semen volume were calculated by four different methods. With the first two methods, the high and low lines were kept separate. The third and fourth methods utilized divergent selection by measuring the response as the difference between the two lines. The realized heritability, calculated as the ratio of the total response divided by the total selection differential for semen volume in the low and high lines,

were $1.47 \pm .40$ and $.35 \pm .08$, respectively. The realized heritability calculated by the regression of the cumulative response on the cumulative selection differential in the low and high lines were $1.34 \pm .42$ and $.41 \pm .08$, respectively. The realized heritability of the total difference in semen volume between lines divided by the total selection differential was $.71 \pm .03$. The realized heritability of the cumulative difference between lines when regressed on the cumulative selection differential was $.68 \pm .06$. This study showed that the heritability of mean semen volume is moderate to high, and that selection for increased semen volume in turkeys was successful.

**Heritability Estimates for Semen Volume
in Medium White Turkeys**

by

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A THESIS

Submitted to

Oregon State University

**In partial fulfillment of
the requirements for the degree of
Master of Science**

Completed July 24, 1987

Commencement June, 1988

APPROVED:

Redacted for Privacy

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Date thesis is presented July 24, 1987

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James A. Harper, Professor Emeritus at the Department of Poultry Science at Oregon State University, started this study, conducted all of the selections and accrued the data needed for this thesis from 1974 to 1982.

ACKNOWLEDGEMENTS

The author wishes to thank the Chester M. Wilcox Memorial Scholarship fund without whose financial help this thesis would not have been possible. I would also like to thank the professors, staff and fellow students, in the Department of Poultry Science at Oregon State University, for making my studies pleasurable. I would like to extend my appreciation to Dr. T. F. Savage for his patience, understanding and help with all of the minor, and major, problems for the last two years. Finally, I would like to thank my parents for always being there when I needed them and letting me take over their computer for the writing of this paper.

TABLE OF CONTENTS

<u>CHAPTER</u>	<u>PAGE</u>
I. INTRODUCTION	1
II. REVIEW OF LITERATURE	3
A. Definition of Heritability	3
B. Importance of Heritability Estimates	4
C. Calculation	5
1. Methods	5
2. Precision	6
3. Biases	7
D. Behavior	12
1. Dependencies	12
2. Reduced Variation	13
E. Selection	13
1. Uses	13
2. Behavior	14
3. Limitations	15
F. Male Fertility	16
1. Importance	16
2. Factors Involved	17
3. Heritability Estimates	19
4. Correlations With Other Traits	28
5. Conclusions	31
6. Summary	31
III. HERITABILITY ESTIMATES FOR SEMEN VOLUME IN MEDIUM WHITE TURKEYS	33
ABSTRACT	34
INTRODUCTION	36
MATERIALS AND METHODS	37

TABLE OF CONTENTS, Cont.

<u>CHAPTER</u>	<u>PAGE</u>
RESULTS AND DISCUSSION	42
REFERENCES	50
IV. BIBLIOGRAPHY	52

LIST OF FIGURES

<u>FIGURE</u>		<u>PAGE</u>
III.1	Response to selection for mean semen volume.	43
III.2	The regression of cumulative response to cumulative selection differential.	46

LIST OF TABLES

<u>TABLE</u>		<u>PAGE</u>
II.1	Heritability of semen traits in chickens	20
II.2	Heritability of fertility with long-term holding of semen.	22
II.3	Repeatabilities of semen traits.	23
II.4	Heritability of testes weight.	24
II.5	Heritability of male aggressiveness.	25
II.6	Range of heritability estimates reported for the turkey.	26
II.7	Heritability of semen traits under selection for semen volume.	27
II.8	Correlations of chicken semen traits with fertility.	28
II.9	Correlations of turkey semen traits to fertility.	29
III.1	Mean heritability estimates for mean semen volume and packed sperm volume.	44
III.2	Realized heritabilities obtained by different methods of calculation.	47

HERITABILITY ESTIMATES FOR SEMEN VOLUME IN MEDIUM WHITE TURKEYS

CHAPTER I

INTRODUCTION

Semen volume is a essential trait in turkey reproduction, hence in turkey breeding operations. Artificial insemination must be used to reproduce market turkeys since adequate fertility cannot be accomplished through natural matings. Larger semen volumes are desirable because fewer males are then required to be bred with a given number of hens. This results in lower maintenance costs for the male side of the breeding operation, and greater selection pressure may be applied to the males.

Heritability (h^2) is one method to determine the feasibility of selecting for a particular trait in a breeding program. The definition of heritability, in the narrow sense, equates it to the breeding value of an animal. The heritability plays an important role in estimating the gain which may be realized through selection. It also may be used to aid in the decision of which mating scheme should be used since different methods vary in their efficiency depending on the heritability of the trait.

The purpose of this study was to determine heritability estimates of semen volume in a selection program, and thus the feasibility of selection for semen

volume in the male turkey. To accomplish this, a strain of medium white turkeys were divergently selected for semen volume over thirteen generations. Their semen was evaluated and the heritabilities were calculated using five different methods.

The results of this experiment show that the heritability of semen volume is moderate to high. Therefore, gains may be rapidly realized under a selection program for semen volume. Given the current methods of reproducing turkeys in the industry, this study shows that it would be logical to select for increased semen volume as well as for other traits.

CHAPTER II

REVIEW OF LITERATURE

A. DEFINITION OF HERITABILITY

Heritability is defined as the ratio of genetic to phenotypic variance for a particular trait. It may be defined in either the broad or the narrow sense. In the broad sense, heritability is defined as

$$h^2 = \frac{\sigma_G^2}{\sigma_P^2}$$

Where σ_G^2 is the genetic variance and σ_P^2 is phenotypic variance. It is the proportion of the total variance due to the differences among the genotypes of the individuals in the population. For practical uses, it is normally assumed that the genetic variance is equivalent to the additive genetic variance.

Thus, the proportion of total variance due to the breeding values of the individuals in the population is measured as

$$h^2 = \frac{\sigma_A^2}{\sigma_P^2}$$

Where σ_A^2 is additive genetic variance. This variance

proportion is referred to as heritability in the narrow sense (Van Vleck, 1973, 1987.)

An equivalent method of obtaining a heritability estimate is by regression of the breeding value to the phenotypic value. By using this method, an estimation of an individual's true breeding value may be obtained:

$$\text{expected breeding value} = h^2 \times \text{phenotypic value}$$

In this equation, the heritability estimate gives the degree of correspondence between the phenotypic and breeding values. It is commonly referred to as the realized heritability of a trait (Falconer, 1985).

B. IMPORTANCE OF HERITABILITY ESTIMATES

As one may assume from its definition, heritability is an extremely important parameter for studies in quantitative genetics. It is of paramount importance to the breeder because it provides an estimate of the proportion of the phenotypic variance which is due to additive genetic variance, thus allowing the breeder to predict the breeding value of a bird from its phenotype. A heritability estimate may also be used to quantitate the amount of flock improvement which may be realized through selection thereby allowing the breeder to predict

the mean phenotype of the next generation (Kinney, 1969; Falconer, 1985; Van Vleck, 1987). Heritability may also aid in the choice of which type of selection program to use for the improvement of the trait of interest (Kinney, 1969).

C. CALCULATION

1. Methods of Calculating Heritabilities

There are several methods that can be used to obtain a heritability estimate. Six of the most common methods are:

- 1. Paternal half-sib correlation**
- 2. Maternal half-sib correlation**
- 3. Full sib correlation**
- 4. Parent-offspring regression**
- 5. Realized heritability**
- 6. Maximum Likelihood approach**

Each of these methods has its own biases and constraints, therefore not all of the methods may be applicable to every situation (Kinney, 1969; Hill, 1971, 1972a).

There is another type of heritability value, the realized heritability, which is directly based on the

response to the selection practiced in the flock. It is defined as the response to selection divided by the selection differential required in order to achieve this response. Four of the more common methods of calculating the realized heritabilities are:

1. the ratio of the total response to the total selection differential
2. the regression of the cumulative response on the cumulative selection differential for each generation
3. the regression of the individual generation response to the individual selection differentials
4. a maximum likelihood approach

These methods may also be used to obtain h^2 from combined data for a divergently selected trait. The different methods of calculating the realized heritabilities also have their own biases and constraints associated with them (Hill, 1971, 1972a, 1972b).

2. Precision

The precision of the heritability estimate is given by its standard error (SE) also known as the sample standard deviation ($\hat{\sigma}$). The sample standard deviation

is used to estimate the population standard deviation (σ) because the population standard deviation is an unknown parameter. One of the difficulties encountered in selection studies is that the standard errors are normally undesirably large because it is difficult to use large enough sample sizes in a breeding experiment (Falconer, 1985).

3. Biases

As mentioned earlier, each of the aforementioned methods of calculation has its own assumptions and biases. Often, these biases can be corrected by making the appropriate adjustment in the design of the study or method of calculating the heritability estimate or the realized heritability of a trait. However, sometimes another approach is necessary in order to correct the bias. Remember, a bias is usually more important than the precision when considering the accuracy of these estimates or determining which estimate to use (Hill, 1971, 1972a, 1972b).

Heritability is estimated from the degree of resemblance between relatives. Therefore, in general, the closer the relationship the more accurate the estimate (Falconer, 1985). It must be remembered that "relatively" large family sizes are necessary when

estimating heritability accurately with any of the sib correlation methods (Robertson, 1959). Also, if non additive variation is important, such as variation due to epistasis, these same methods will result in a heritability estimate which is biased upward (Kinney, 1969).

The next question to be answered is which of the three correlation methods tends to give the more accurate estimate of heritability. The paternal half-sib correlation method appears to be the most accurate of the three correlation methods because it is not influenced by the maternal effects nor the dominance variation of the dam in the hierarchal mating structure (Kinney, 1969; Falconer, 1985). There is disagreement on whether the maternal half-sib or the full-sib correlation is less biased. Kinney (1969) and Van Vleck (1987) believe that the full sib correlation method is intermediate, between the paternal and maternal half-sib correlations, in both values and biases. Falconer (1985) reports that the full-sib correlation method is the most biased of the correlation methods of calculation and can only be used to set the upper limits of heritability due to maternal effects. This difference in opinion might have arisen because Kinney and Van Vleck were studying poultry and Falconer studied laboratory mice. Maternal effects have a much greater impact in heritability studies dealing

with mammals when compared to those with poultry.

The parent-offspring regression and the realized heritability are the most accurate of the five more commonly used methods for determining heritability estimates (Kinney, 1969). The regression of half-sib offspring to the sire is considered to be more reliable than the regression of the half-sib to the dam or the full sib regression to either the sire or the dam. This is because the half-sib regression to the father has less maternal effects than either the half-sib regression to the dam or the full-sib regression to either the sire or the dam (Falconer, 1985). The extent of the maternal effects do depend on the organism studied. Poultry has a very small amount of maternal influence, where as mammals have a large maternal influence.

Other factors may warrant consideration before the decision of which heritability estimate to use in a selection program. There are additional shortfalls associated with each of the previously discussed methods. The intra-class correlation methods do not use the parent's performance, and the parent-offspring regression cannot make use of the differences between family means. Although both of these methods may be used to calculate heritability estimates on the same data, it is usually impossible to pool the estimates (Hill and Nicholas, 1974).

When using the calculation methods which combine the data from divergently selected lines, the response to selection is assumed to be symmetric (Hill, 1979). An asymmetrical response to selection will result in a calculated realized heritability between those of the two lines calculated separately. These asymmetrical responses are quite common in selection experiments, especially in long-term studies (Hill, 1979; Falconer, 1985). There are several possible causes of asymmetry:

1. indirect selection in one direction by either natural or artificial means
2. scalar asymmetry with one line being more susceptible to environmental changes
3. genetic asymmetry with differing gene frequencies, dominance deviation or genes with large effects
4. random drift
5. inbreeding depression
6. maternal effects
7. environmental trends

Any or all of these factors may contribute to an asymmetrical response to selection (Falconer, 1985). Usually, a heritability estimate derived from a divergent selection program will overestimate heritability of the high line, which is also the direction that is most

commonly of interest to the breeder (Hill, 1979; Falconer, 1985). Therefore, a breeder will overestimate his progress when using a heritability estimate derived from divergent selection (Falconer, 1985).

A relatively new method of calculating the heritability estimate is the maximum likelihood approach (ML). This approach may be used to calculate the realized heritability or the standard heritability estimate. Depending on the family sizes used, the duration of the experiment and the true value of the heritability, the ML estimate may be more or less accurate than the standard methods of estimating heritability (Hill, 1971, 1972a; Hill and Nicholas, 1974). If small family sizes are used, either the ML or a pooled heritability estimate based on the parents and progeny is more efficient than the intra-class correlations of progeny alone. The simple estimators of heritability from the regression models are nearly as effective as the those obtained by the ML model and tend to be less biased. In general, the realized heritability is almost as accurate as the ML estimate and more convenient to use (Hill, 1972a; Hill and Nicholas, 1974). Linear regressions of realized heritability also give the advantage of allowing the breeder to predict the likely phenotypic value of the next generation based on the performances of the previous generations.

D. BEHAVIOR

1. Dependencies

The value, of the heritability estimate, depends on the magnitude and the nature of all the variance components of the phenotypic variation. This results in a heritability estimate that is not only dependent on the additive genetic variance, but also the variances within the population and the environment to which the individuals are subjected. Gene frequency also has an impact on the genetic component of variance, and may vary among populations. If either the environmental or genetic component is different between populations, then the heritability estimate will probably be different. Needless to say, a particular heritability estimate for a given trait is good only for the environmental conditions and population used in the derivation of that estimate. Heritability values determined for other populations may be more or less similar according to the similarity in both environment and in the genetic structure of the population (Falconer, 1985; Van Vleck, 1987).

2. Reduced Variation

When estimating heritabilities and genetic correlations on several traits simultaneously, neither selection nor assortative mating is desirable. This is because these practices will reduce the variability between the parents hence the efficiency of the heritability estimates (Hill and Nicholas, 1974). Inbreeding also contributes to a lower heritability estimate, when compared with an equivalent population of randomly breeding individuals (Dempster and Lerner, 1947; Nordskog et al., 1974). As expected from the effects of inbreeding, a smaller population will usually show lower heritabilities than a larger one. This phenomenon is due to gene fixation (Falconer, 1985).

E. SELECTION

1. Uses

The efficiency of a selection program, hence a breeder's operation, depends on three major factors:

1. intensity of selection
2. accuracy of selection
3. average interval between generations

The accuracy of the selection for a trait is proportional to the heritability for that trait (Dempster and Lerner, 1947). Therefore, heritability plays an important role in a selection program for quantitative traits.

The magnitude of the heritability estimate can aid the breeder in deciding which selection program would be more efficient for improving a particular trait. If the trait is highly heritable, the most economical and rapid improvement will be made via mass selection. Progeny testing and family selection is more efficient when the trait has a low heritability (Kinney, 1969).

2. Behavior

Selection, especially for a moderate to highly heritable trait, will tend to bias the heritability estimate downward, sometimes by as much as 50%. This is because selection reduces the variance between the parents, hence the covariance among the siblings (Nordskog et al., 1974; Falconer, 1985). If the selection is based on the same trait as the heritability estimate, the regression of offspring to parent is not affected, but the precision is reduced because of lower variability between the parents. Divergent selection can improve the precision of the heritability estimate if the offspring of the two lines are reared together and only the

offspring of the selected parents are reared (Falconer, 1985). One must be cautious when using a divergent selection program to obtain a realized heritability by regressing the cumulative differences between the lines to the cumulative selection differentials. The reason for the caution is that an asymmetric response to selection will bias the calculated heritability upward for most economically important traits and, as a result, the expected flock improvement may be overestimated. This same phenomenon will also bias most methods of calculating heritability estimates in one direction (Falconer, 1954).

Lowering of the heritability estimate due to exhaustion of genetic variation is possible and may be responsible for the lowering of genetic gains (plateauing) made in a particular trait over time. More likely, other factors will play a greater role in the deceleration of genetic gains long before the limitations imposed by decreasing genetic variability (Lerner and Dempster, 1951; Nordskog et al., 1974; Dickerson et al., 1983).

3. Limitations

If the heritability estimate is to be accurately predicted, it must be derived from the same population in

which the estimate is to be used and it must be for a for a relatively short time interval. The reason for the time constraint is that heritability can be fairly accurately predicted on a short-term basis, but not when selection is conducted for several generations because theory requires large population sizes as a major assumption and this assumption is rarely achieved in an actual flock (Kinney, 1969; Nordskog et al., 1974).

F. MALE FERTILITY

1. Importance

The male plays a dominant role in the fertility of poultry flocks (Kamar, 1960). There is a positive relationship between net chick production and its cost, thus creating a considerable economic value for selecting highly fertile males. This holds true for both meat and egg type birds. In White Leghorns, the male is considered to be largely responsible for infertility. For naturally breeding populations, sex drive, as well as semen quantity and quality, plays a role in fertility. All of these factors are regulated by multiple genetic loci, thus heritability estimates may be derived and improvement through selection is possible.

The economic importance of fertility is also true in turkeys. Because of the extensive use of artificial insemination, turkey semen must be of good quality and quantity. Larger quantity of semen allows for more inseminations and thus a greater number of hens per tom. Quality is also important because of the use of semen extenders (McCartney and Brown, 1958; Brown, 1970b). Since the concentration of sperm is now a factor, methods of its determination have been established. Three of the most common methods which accurately estimate sperm concentration are:

1. optical density
2. hemocytometer
3. packed sperm cell volume

Any of these methods can be used to accurately estimate sperm concentration in poultry semen (Taneja and Gowe, 1961).

2. Factors

In addition to semen characteristics, there are other factors which affect male fertility. Fertility is influenced by environmental, social, anatomical, physiological and genetic factors (Kamar, 1960). Some

environmental factors which affect fertility in chickens and turkeys are semen collection (Brown, 1970b), lighting (Nestor et al., 1970a; Nestor et al., 1970c; Krueger et al., 1977), age of bird (Carson et al., 1955b; Nestor, 1970a), and the feeding program (Nestor et al., 1970b). An important anatomical factor affecting male fertility is body weight (Krueger et al., 1977). There has been intense genetic selection for increased body weight in the market turkey, primarily for increased breast muscle, resulting in walking difficulties in the breeder toms. If selection is conducted for increased shank width, this problem will be alleviated. Selection for shank width can easily be accomplished since it has a heritability estimate of approximately $.33 \pm .05$ (Nestor et al., 1985).

Since genetics has a prominent role in several of the factors contributing to male fertility in the chicken and turkey, it would follow that heritability estimates could be used to aid in selection programs designed to increase male fertility.

3. Heritability Estimates

As mentioned earlier in this paper, the heritability estimate will vary depending on the population of birds and previous selection practices. This section shows some of the variation in the heritability estimates reported for traits affecting male fertility in the chicken and turkey. The following are the abbreviations and methods by which the heritability estimate may be derived:

- | | |
|--------------------------------|-----|
| 1. Paternal-sib correlation | P |
| 2. Maternal-sib correlation | M |
| 3. Full sib correlation | F |
| 4. Parent-offspring regression | P-O |
| 5. Realized heritability | R |
| 6. Maximum likelihood | ML |

CHICKEN

Table II.1. Heritability of Semen Traits in Chickens.

Heritability Estimates			Method	Reference
Volume Concentration Motility				
.14	.01	.29	F	Seigel, 1963
.41	.46	.87	P	Soller <u>et al</u> , 1965b
.34	.37	---	ML	Ansah <u>et al</u> , 1985
.64	.65	---	ML	Ansah <u>et al</u> , 1985

The studies summarized in Table II.1 did not emphasize selection for semen characteristics, although selection for other traits did occur. Seigel (1963) selected for breast angle. Soller et al. (1965b) did not indicate the selection practices for the flock that he used to calculate his heritability estimates. The standard errors of Soller's (1965b) heritability estimates were .30 for all three semen traits. The first set of heritability estimates reported by Ansah et al. (1985) was derived from a population selected for the duration of frozen-thawed semen. The second set of

heritability estimates reported by Ansah et al. (1985) were from the control birds of the same study. Ansah et al. (1985) reported that the difference between the heritabilities of the control and selected lines may indicate that selection for some semen traits may be necessary if fertility is to remain constant when selecting for the duration of frozen-thawed semen. There is considerable variation between the heritability estimates reported by Seigel (1963) and those reported by Soller et al. (1965b) and Ansah et al. (1985). I believe that Seigel's (1963) study showed atypical findings due to unusual environmental conditions or lower than normal genetic variation for a poultry flock. Without further information, a logical conclusion cannot be formed. The few available studies on semen volume, and to a lesser degree concentration, in chickens indicate that moderate to high heritabilities is probably the norm. These strong heritabilities indicate that improvement of semen traits, through selection, should be quite successful.

Table 11.2. Heritability of fertility with long-term holding of semen.

	Frozen-Thawed		Fresh	
	selected	control	selected	control
duration of fert. ¹	.12	--	--	--
% fertility ¹	.09	--	--	--
duration of fert. ²	.21	.24	.04	.03
% fertility ²	.09	.31	.01	.06
% hatch of fert. ²	-.01	.25	--	--

1. Mitchell et al., 1977

2. Ansah et al., 1983

The heritability estimates for fertility in a line of chickens selected for the duration of fertility from frozen-thawed semen and its control line are summarized in Table 11.2. The same two lines of birds were used for both studies and the heritabilities were calculated using the regression of son on sire (Mitchell et al., 1977; Ansah et al., 1983). Note, the heritability estimates for these fertility traits are relatively low, especially when compared to the heritability estimates of most of the semen traits.

Table 11.3. Repeatabilities of semen traits.

Volume Concentration Motility			
			<u>Type of Bird</u>
.90	.81	.84	Cornish ¹
.80	.82	.83	White Plymouth Rock ¹
.78	.79	.87	White Plymouth Rock ²
			<u>Selection</u>
.95	.51	.33	low growth rate ³
.90	.74	.66	high growth rate ³
.35	.33	--	duration of fertility\ frozen-thawed semen ⁴
.48	.45	--	control birds

1. Soller et al., 1965a

2. Soller et al., 1965b

3. Marini and Goodman, 1969

4. Ansah et al., 1985

Since repeatability may be used to denote the upper extreme of a possible heritability estimate (Ansah et al., 1985), the repeatability of a trait may be compared to a calculated heritability estimate to assist in determining if the heritability estimate is within the realm of possibility. Table 11.3 summarizes the repeatability values for chicken semen traits. The repeatability

values for volume, concentration and motility are quite strong in these studies (Soller et al., 1965b; Ansah et al., 1985).

Table 11.4. Heritability of Testes Weight

Age	h^2	Method
1 day	.70	F
11 days	.60	F
62 days	-.18	F
11 weeks	.43	F
11 weeks	.47	P/O (on sire)

Kinney, 1969

Table 11.4 summarizes the heritability of testes weight and shows that the heritability of testes weight is fairly large. This indicates that a selection program for testes weight is possible and may be advantageous if testes weight is correlated to semen production.

Table II.5. Heritability of Male Aggressiveness

Matings Completed		
h²	SE	Method
.52	--	M
.33	--	F
.18	.05	R
.31	.11	R

Kinney, 1969

The heritability estimates for male aggressiveness were based on the number of matings completed in a specified time. These heritability estimates, summarized in Table II.5, indicate that selection for mating aggressiveness is possible. In some naturally mating populations, it may be helpful to select for this trait.

TURKEY

Table 11.6. Range of Heritability Estimates reported for the Turkey.

Trait	Method of Calculation		
	P	M	F
mean volume/ejaculate	1.00	.28-.37	.86
total volume produced	.20-1.00	.04-.40	.19-.89
mean conc. (visual)	.34-.88	.44-.69	.39-.79

Carson et al., 1955b

Carson et al. (1955b) determined the heritability estimate for semen traits in Broad Breasted Bronze turkeys using no selection with respect to the semen traits. There was considerable variability between the heritability estimates calculated (Table 11.6). Carson (1955b) reported that most of this variation in heritability estimates was due to small family sizes. He also concluded that a substantial part of the phenotypic variation of semen volume was due to heredity.

Table 11.7. Heritability of semen traits under selection for semen yield.

Trait	Generation	h^2	SE	Method
semen volume ¹	4	.64	.08	F
concentration ¹	4	.16	.03	F
% abnormal sperm ¹	4	.18	.03	F
mean volume ¹	4	.40	.23	R
mean volume ²	5	.35	.20	R

1. Nestor, 1970b

2. Nestor, 1974a

Nestor (1970b, 1974a) determined heritability estimates of semen traits using medium white turkeys that had been selected for increased semen yield early in the breeding season (Table 11.7). He maintained a randomly mated control population to compare to his selected line. The two realized heritabilities were obtained by dividing the response to selection by the selection differential in different years (Nestor, 1970b). He concluded that selection for semen yield had been successful in increasing semen ejaculate volume without a change in sperm concentration, percent abnormal sperm, percent fertility, percent hatch of fertile eggs, or number of poults produced per hen in a 12-week hatching period

(Nestor, 1974a). This study indicated that selection for semen yield, in turkeys was feasible.

4. Correlations with Other Traits

There are several important traits that are significantly correlated with semen quality and/or quantity in both chickens and turkeys. Semen volume, concentration and motility have high, positive phenotypic correlations with each other (McDaniel and Craig, 1959). Since semen traits may be indirect measures of male fertility, the correlations between these traits and fertility may be useful in a selection program.

Table II.B. Correlations of chicken semen traits with fertility.

Volume	Concentration	Motility	Reference
.14	--	.84	Cooper and Rowell, 1958
.13	.04	.14	Soller <u>et al.</u> , 1965a*
.09	.46	.64	Soller <u>et al.</u> , 1965a

*natural matings were used, others were artificial insemination

Table II.B summarizes the correlations of semen traits with fertility in the chicken. With natural matings, the correlations between the semen traits and

fertility are low. Correlations of fertility with sperm concentration, and especially sperm motility, are high when artificial inseminations were used. These high correlations indicate that sperm motility may play an important role in fertility when artificial insemination is used (Soller et al., 1965a). Since all of the semen traits described above are positively correlated to fertility, selecting for any of these traits may improve the fertility of the flock.

Table II.9 Correlations of turkey semen traits to fertility.

semen volume	.31
visual density	.34
semen volume and visual density	.45

Brown, 1970a

The moderate correlations of semen traits and fertility in the turkey, Table II.9, indicate that the number of hens inseminated per ejaculate can be increased by selecting for semen volume. Fertility may also be increased through selection for semen volume (Brown, 1970a). The correlations of semen volume to fertility in the turkey are higher than those reported for chickens, indicating that concurrent selection for semen volume and

fertility in turkeys might be more effective than in chickens.

Although embryonic survival in chickens does not have a significant correlation to semen characteristics, there is some evidence to suggest that hatchability does depend somewhat on sperm quality (Cooper and Rowell, 1958). Semen concentration significantly correlates with sexual aggressiveness behavior (McDaniel and Craig, 1959).

There is data suggesting that egg production in the female is positively correlated to semen production, and perhaps packed sperm volume, in male turkeys and chickens (Jones and Lamoreux, 1942; Marks, 1978). The theory to support these observations is that both the males and females are subjected to the same endocrine control, thus an increase in hen egg production may result in a concurrent increase in male sperm volume, and vice-versa. If this correlation is maintained over time, it could be useful when selecting for increased egg production in females (Jones and Lamoreux, 1942; Nestor, 1970b; Nestor, 1974b; Marks, 1978). However, there may be some difficulty with using this correlation with turkeys, Nestor (1970b) reported that the increase occurred during the first year of selection, and then the selected line lost its superiority with each successive generation. He concluded that the initial increase was probably due more to linkages than a strong genetic correlation.

5. Conclusions

Other reproductive traits, such as egg production, fertility and hatch of fertile, have low heritabilities (Falconer, 1985), but most semen traits have strong heritabilities. That means that selection based on male fertility is not only possible, but economically advantageous. Therefore, when breeding for increased fertility, it might be beneficial to test males for their fertilizing ability because most traits are transmitted to their sons (Kamar, 1960), and perhaps even their daughters (Jones and Lamoreux, 1942; Marks, 1978). A male selection index, utilizing both semen and behavioral traits, would probably be an efficient system to use (McDaniel and Craig, 1959).

6. SUMMARY

Heritability estimates can be a valuable part of a selection program. They can assist the breeder in determining the method of selection that would be the most efficient under given conditions relevant to his flock. Heritability estimates may also be used to gauge the amount of improvement possible for a given trait of interest thus allowing for the forecasting of genetic improvement.

Semen quantity and quality should be looked at as traits of economic importance and should be selected for. If semen yield can be increased, so can the number of females inseminated per male. This could result in fewer males having to be maintained, hence lower costs and the possibility of a greater selection differential for these and other traits.

CHAPTER III

HERITABILITY ESTIMATES FOR SEMEN VOLUME
IN MEDIUM WHITE TURKEYS

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ABSTRACT

A population of Wrolstad strain Medium White turkeys has been divergently selected for low and high mean semen volume for 13 generations. A mean volume difference of .34 mls. was obtained in the 13th generation; with the low line averaging .21 mls. and the high .55 mls. Heritability estimates determined by the full sib correlation method averaged $.61 \pm .13$ and $.54 \pm .15$ for the low and high lines, respectively. Realized heritabilities for semen volume were calculated by four different methods. With the first two methods, the high and low lines were kept separate. The third and fourth methods utilized divergent selection by measuring the response as the difference between the two lines. The realized heritability, calculated as the ratio of the total response divided by the total selection differential for semen volume in the low and high lines, were $1.47 \pm .40$ and $.35 \pm .08$, respectively. The realized heritability calculated by the regression of the cumulative response on the cumulative selection differential in the low and high lines were $1.34 \pm .42$ and $.41 \pm .08$, respectively. The realized heritability of the total difference in semen volume between lines divided by the total selection differential was $.71 \pm .03$. The realized heritability of the cumulative difference between lines when regressed on the cumulative

selection differential was $.68 \pm .06$. This study showed that the heritability of mean semen volume is moderate to high, and that selection for increased semen volume in turkeys was successful.

INTRODUCTION

Genetic selection for improved fertility has an economic consequence because it decreases the production cost of the day old poult. Semen volume affects male fertility and has genetic components which make it possible to calculate heritability estimates (h^2) and make improvement through selection (McDaniel and Craig, 1959; Soller et al., 1965).

Limited heritability estimates have been calculated for semen ejaculate volumes in turkeys. Carson et al. (1955) worked with Broad Breasted Bronze turkeys, and calculated moderate to high heritabilities for semen volume using the correlation between and among family units. Using the full-sib correlation method, Nestor (1970) calculated a heritability of $.64 \pm .08$ for the mean semen volume of medium white turkeys. A realized heritability of $.35 \pm .20$ was calculated based upon five generations of selection (Nestor, 1974). The purpose of this study was to obtain heritability estimates and realized heritabilities of semen volume in a long-term selection program.

MATERIALS AND METHODS

Development of the lines. Two sub-populations of Wrolstad Medium White turkeys were genetically isolated and selected for low (Lo) and high (Hi) semen volume for 13 generations. The process consisted of selecting a minimum of 20 males per generation at 20 weeks of age. The males selected represented four full-brothers from each of five randomly selected pair matings per line. Commencing at 34 weeks of age, the semen was collected and measured from all of the males of each line for three consecutive times within two weeks and mean individual ejaculate volumes were calculated. Two full-brothers from each sire, within a line, with the highest and lowest mean semen volumes, respectively were selected as the breeders of each line (n:10) for the subsequent generation. Semen was then collected and the volume and sperm cell concentration determined biweekly for 12 additional measurements.

The breeder hens, within each line, were selected at random from all pair matings at 20 weeks of age. Each sub-line was reproduced using 100 sire-dam pedigreed matings in which full and half-sib matings were not used. Both lines were housed in the same building containing 20 litter covered floor pens. Each pen measured 9.3 m² and housed 10 hens. Insemination of ten hens per male was

conducted on days 20, 27, and 34 following photostimulation (14L:10D) and inseminations continued thereafter at two week intervals. Undiluted semen was used to inseminate the hens using .025 ml. per hen; however, semen dilution with Beltsville diluent or insemination with less than .025 ml. was sometimes necessary in the low line. Eggs were collected daily using a trapnest pedigree system and marked for identification, dry-cleaned as required, fumigated with formaldehyde gas and stored for up to two weeks at 12.8 C (55 F). Seven to nine biweekly settings of the eggs in a Robbins 17H incubator were conducted to determine fertility and hatchability of the eggs.

Starting at 34 weeks of age, semen was collected from the males using an abdominal massage method. The number of cloacal strokes used varied and were applied until no further semen was ejaculated. Semen was collected into 15 ml plastic cups and the volume was measured to the nearest .01 ml using a tuberculin syringe. Packed sperm volume (PSV), as a measure of sperm cell concentration, was determined by the centrifugation method of Arscott and Kuhns (1969).

Propagation of the two sub lines was accomplished by transferring full pedigreed eggs of two consecutive settings, each generation, to individual hatching baskets at 25 days of incubation. At hatching, all the poults

were individually wing banded and the poultts of the two lines grown together on litter floor pens to 8 weeks of age. The poultts were then transferred to grass covered ranges and reared to 20 weeks of age. The poultts were all fed the appropriate standard OSU turkey rations in mash form.

At 20 weeks of age, a minimum of 20 males per line (four full-brother progeny from each of five different matings) were selected based upon general appearance characteristics. The females were selected from all the females available at 20 weeks of age, except for those whose dams had demonstrated prolonged incidents of broodiness. At this age, the males and females were separated. The males were maintained under natural light until 24 weeks of age, then subjected to a (8L:16D) daily photoperiod until photostimulation commenced four weeks prior to that of the females.

Heritability Estimates. A one-way analysis of variance (ANOVA) was performed (Sincich, 1985) and the variance components between and among families were calculated for mean semen volume. The heritability estimate per line was calculated from the variance components using the full-sib correlation method (Becker, 1985). These yearly heritability estimates were then averaged within each of the two lines to provide an overall mean heritability estimate for the 13 generations

of selection. This same method was used to calculate the heritability estimates for packed sperm volume.

Realized Heritabilities. The realized heritabilities were calculated using four different methods. In the first two methods, the realized heritabilities of the high and low lines were calculated separately, as two distinct populations. The ratio of total response to selection was divided by the total selection differential needed to achieve the response, for each line. The second method of calculating the realized heritability consisted of simple linear regression (Sincich, 1985) of the cumulative response to selection against the cumulative selection differential (Falconer, 1954). Standard errors of the realized heritabilities for these two methods were calculated using the method described by Hill (1972b), which adjusts for random drift and error variance.

The third and fourth methods of calculating the realized heritability of mean semen volume involved measuring the response as the difference, in volume, between the low and high lines and combining the two selection differentials. Combining the data from two divergently selected lines decreases the amount of environmental variation in the calculation of the realized heritability. The third method divided the

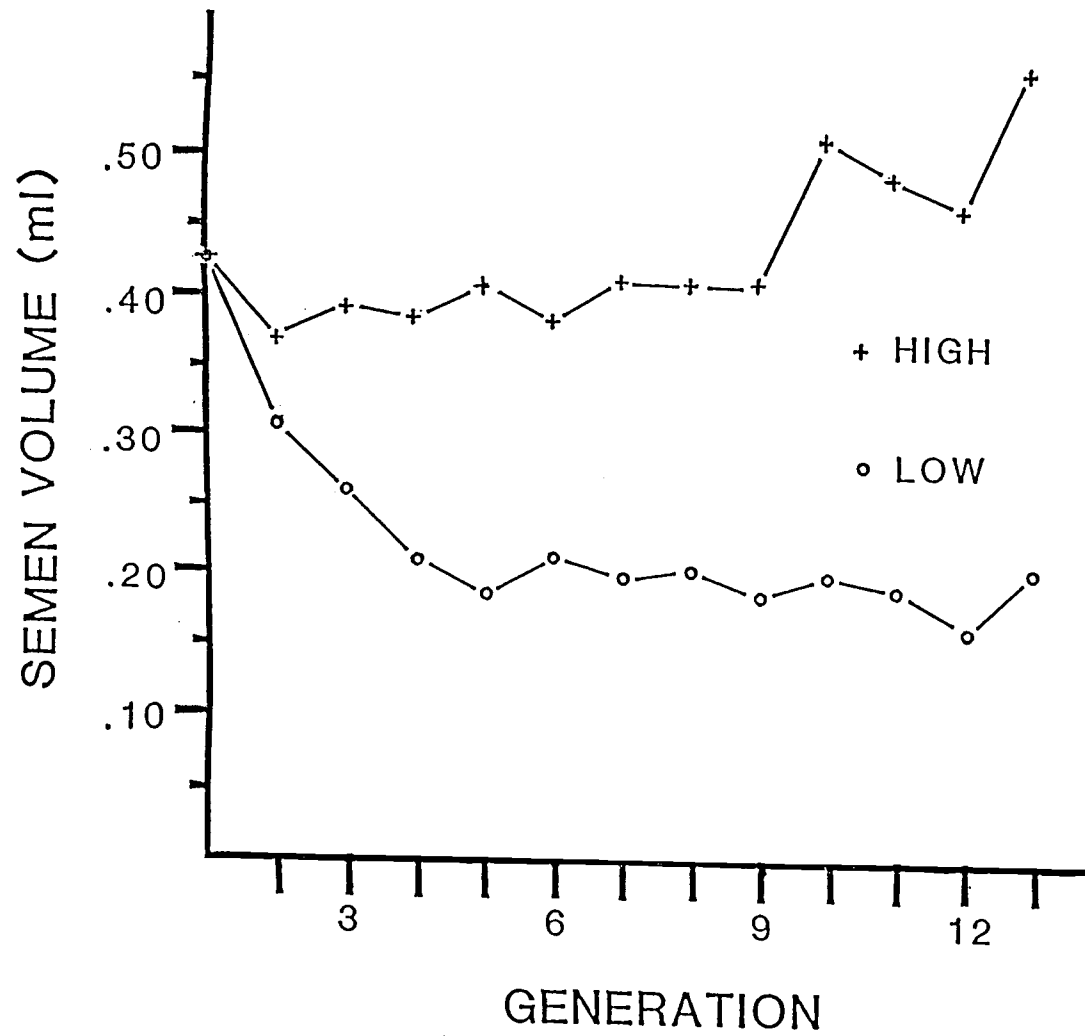
difference in semen volume between the lines in generation 13 by the total selection differential of the two lines (Hill, 1972a). With the fourth method, the cumulative difference, in semen volume between the lines, per generation was regressed on the cumulative selection differential. The standard errors were calculated using the formula described by Hill (1972a). Realized heritabilities were not calculated for packed sperm volume because direct selection pressure was not applied.

RESULTS AND DISCUSSION

The progress achieved by divergently selecting for high and low mean semen volume is summarized in Figure 1. The base population's mean semen volume was .43 mls. per ejaculate. The semen volume difference between the two divergently selected lines has increased from generation two onward, with greater progress occurring in the low line. A negative change of .22 mls. is observed when comparing generation one to the generation 13 in the low line. The high line had a mean volume of .55 ml. in generation 13, an increase of .12 mls. when compared to generation 1. The difference between the high and low lines in generation 13 was .34 mls. There was variability of response to selection between generations of selection. This variability in semen volume was probably due to environmental effects since the birds were range reared and then housed in non-environmentally controlled facilities. There were environmental fluctuations over the years, but no climatic trend was found (Redmond, 1986).

The heritability estimates using the full-sib correlation method are shown in Table 1. The mean heritability estimate for mean semen volume over the 13 generations was $.61 \pm .13$ and $.54 \pm .15$ for the low and

FIGURE III.1. Response to selection for mean semen volume.



high lines, respectively. There was no significant difference between the two heritability estimates. The heritability estimate for the high line, using the full-sib correlation method, was not significantly different from Nestor's (1970) estimate of $.64 \pm .08$ using similar birds and experimental design, but the estimate was lower than Carson's (1955) estimate of .86 using Broad Breasted Bronze turkeys. The average heritability estimate determined for the packed sperm volume in the high line was $.47 \pm .16$, much larger than Nestor's (1970) estimate of $.16 \pm .03$, but was within the range of Carson's (1955) estimates. There was variation in the heritability estimates, of the packed sperm volume, for the different generations.

Table III.1. Mean heritability estimates for mean semen volume and packed sperm volume.

Trait	Line	h^2	SE	95% CI*
Volume	Lo	.61	.13	.33 - .88
	Hi	.54	.15	.21 - .86
PSV	Lo	.60	.19	.18 - 1.02
	Hi	.47	.17	.10 - .83

* CI = Confidence Interval

Least squares regression lines for the mean semen volume in the low and high lines are shown in Figure III.2. The slope of the regression lines (1.34 and .41 for the low and high lines, respectively) were used to calculate the realized heritability of each of the two sub-lines by the second method. The realized heritabilities obtained by the four methods are summarized in Table III.2. The realized heritability obtained by dividing the total response by the total selection differential in the high line alone was $.35 \pm .08$, which is the same as Nestor's (1974) estimate of $.35 \pm .20$. The estimate of $.41 \pm .08$ obtained by regressing the cumulative increase in semen volume on the cumulative selection differential was not significantly different than the estimate of $.35 \pm .08$ obtained by the first method.

Figure III.2. The regression of cumulative response to cumulative selection differential.

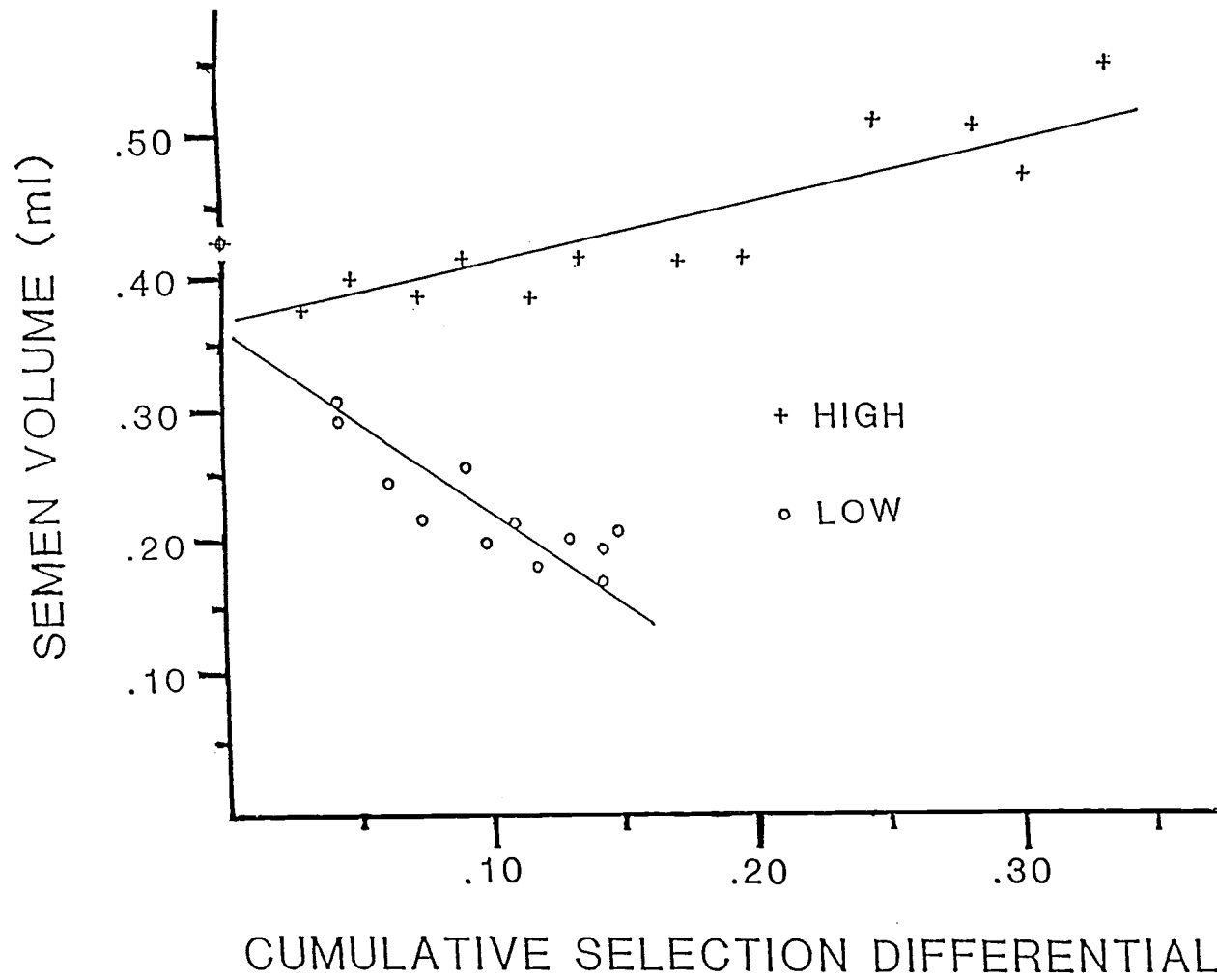


Table III.2. The realized heritabilities obtained by different methods of calculation.

Method of Calculation	h^2	SE
Total response divided by total selection differential		
Low	1.47	.40
High	.35	.08
Divergent	.71	.03
Regression of cumulative response to cumulative selection differential		
Low	1.34	.42
High	.41	.08
Divergent	.68	.06

The calculated realized heritabilities for the low line were above 1.0, using both the ratio and the regression methods. Although this is theoretically impossible, it has been known to occur.

There are several possible causes for an asymmetrical response in a selection study. If the selected trait has an increased natural fitness associated with it, this trait will show a slower response to artificial selection compared to selection for decreased fitness (Falconer, 1985). Natural

selection should favor increased semen production, so this may be a factor. Random drift may be a factor since the selected lines were not replicated. Genetic asymmetry is a possibility, either the initial gene frequency, the dominance deviation or a combination of both may contribute to the asymmetry (Falconer, 1985). Any of these factors would result in an asymmetrical response to selection, and several may be impacting this study. Therefore, there is a good chance that genetic factors have a larger impact on the asymmetrical response to selection than the environmental factors. A downward environmental trend cannot be ruled out because an unselected control line was not available. The environmental variance fluctuated from year to year, but a climatic trend was not observed. Examination of the climatology data for Corvallis indicates no such macroenvironmental trend (Redmond, 1986) and neither the breeder management nor facilities were changed during the study.

If a divergent selection program is to be used to derive a realized heritability estimate, then symmetrical response to selection is a major assumption (Hill, 1979). There is evidence to suggest that this method is inaccurate due to the asymmetrical response. Another factor to consider is that selection will be for increased semen volume, not decreased volume. Using the

realized heritability estimate from divergent selection will tend to overstate the projected progress made in the selection program for the following year (Falconer, 1985). Therefore, those estimates for increased semen volume (Hi line) are more applicable for commercial applications.

There are advantages to both methods of obtaining realized heritabilities, thus it is difficult to determine which value may be more accurate. The regression of cumulative response on the cumulative selection differential is probably the most accurate since a control line was not available and this method provides less biased results in the absence of a control (Hill, 1971). The ratio of total response to total selection differential is more efficient when $h^2 > .40$ but the difference in the accuracy of the estimate is not large (Hill, 1972b) and the heritability for semen volume is very close to .40. With either method, the realized heritabilities are comparable.

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CHAPTER IV

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