INHERITANCE OF NUMBERS OF LATERAL PLATES AND GILL RAKERS IN *GASTEROSTEUS ACULEATUS*

D. W. HAGEN*

College of Fisheries, University of Washington, Seattle, Washington 98195

Received 23.v.72

SUMMARY

Heritabilities for lateral plates in *Gasterosteus* are 0.50 ± 0.043 at 21° C. and 0.83 ± 0.033 at 16° C. for Lake Wapato stocks, and 0.84 ± 0.039 at 21° C. for five other populations. The estimate for gill rakers from Lake Wapato is 0.58 ± 0.056 at 21° C. In general, the two sexes of offspring do not differ in heritabilities; maternal effects apparently are not present. There is evidence that the asymmetry of plates has a large genetic component. The heritability is estimated at 0.63 ± 0.16 . Sex ratio varies widely among laboratory-reared families and there is a significant excess of females in the field. No effects of temperature or density on sex ratio were found.

1. INTRODUCTION

SINCE the classic monographs of Bertin (1925) and Heuts (1947a) the remarkable variability of the threespine stickleback (*Gasterosteus aculeatus*) has attracted attention, particularly the variability in number of lateral plates and gill rakers (Hubbs, 1929; Heuts, 1947a, b, 1956; Lindsey, 1962; Munzing, 1963; Hagen, 1967; Miller and Hubbs, 1969). Almost all the variation in sticklebacks has been attributed to hybridisation and introgression (Munzing, 1963; Miller and Hubbs, 1969), but Hagen (1967), Hagen and McPhail (1970), and Hagen and Gilbertson (1972) found that hybridisation is largely confined to narrow zones in some coastal streams in the Pacific Northwest, America. Apparently introgression does not occur in the area, or at most is of minor importance as a cause of variation.

On the other hand, recent geographic surveys, work on natural populations and estimates of the intensity of selection in freshwater populations indicate that natural selection is a major cause of variation. Differential predation is probably one of the major selective agents acting on the variation among individuals for plates, whereas feeding specialisation in diverse habitats is a major selective agent acting on the variation in gill rakers (Hagen and Gilbertson, 1972, 1973; Moodie, 1972; Moodie, McPhail and Hagen, 1973; McPhail, unpublished data).

Implicit in all these studies is the assumption that these traits have a genetical basis. The purpose of this paper is to give estimates of heritability for number of lateral plates and gill rakers in *Gasterosteus*.

2. MATERIALS AND METHODS

Three plate morphs can be distinguished in freshwater sticklebacks (*leiurus*), which we have simply named the low, partial and completely

* Present address: Biology Department, University of New Brunswick, Fredericton, New Brunswick, Canada.

plated morphs. These three morphs have been illustrated and discussed elsewhere (Hagen and Gilbertson, 1972, 1973). They are controlled by major genes, and data on their genetics will be given in another paper. Within each morph the number of plates varies. For example, in freshwater sticklebacks that are monomorphic for the low plated morph, plate number varies from zero to 14. It is this variation in plate number that concerns us here. Like plate number, the gill rakers on the first gill arch vary widely within and among populations. For example, the mean may be as low as 14.6 in some populations or as great as 21.7 in others (Hagen and Gilbertson, 1972).

The estimates of heritability for these traits are based on 95 families reared in the laboratory. Seventy-seven families were obtained with stocks from Lake Wapato in 1968 and 1969, and the heritabilities were estimated by the usual method of regression. The remaining 18 families were obtained in 1970 with stocks from Lake Quinault, Scatter Creek, Conner Creek,

FIG. 1.—Lateral plates of *Gasterosteus*. Number varies from 3 to 14 in the populations used for heritability studies.

Chinacum Creek and the Samish River. All families were obtained by crossing parents from within localities (no crosses were made between localities), and the heritability was estimated by regression using offspring and parents from all five localities. Details of these populations are given in the papers of Hagen and Gilbertson (1972, 1973), and all are freshwater sticklebacks. The number of gill rakers in these populations varies from 12 to 26, and the number of anterior plates (fig. 1) varies from 3 to 14. These populations were chosen because of the great variation in number of plates and rakers in Lake Wapato, and because the others show large differences in mean number of plates among the populations.

Stocks of adults were gathered in the field during May and June when large numbers of gravid females and mature males are available, and they were transported to the laboratory in styrofoam containers. Matings between parents were made in the laboratory as soon as adults were collected. Eggs of mature females were artificially expressed into a small petri dish (25 mm.) containing a few drops of lake water by gently pressing the abdomen, and the testes of a male were immediately removed from a slit in the coelom and finely chopped with forceps in the dish. The clutch of eggs was then divided into about equal halves before the egg shell hardened, and half the clutch was discarded.

The clutch size of the females used is greater than 40. Such large numbers of progeny in aquaria produce crowding and mortality. Falconer (1960) discusses the problems of experimental design for heritability estimates, as to whether one should use few large families or many small ones with the available facilities. Sampling error of the estimate will depend upon the magnitude of the heritability, but even with low heritabilities a large number of families each of about five progeny will give a reasonably precise estimate. In fact, most of the families I obtained with half clutches were much greater than this and none was less than eight.

Families were reared as uniformly as possible, each in 61-litre aquaria holding lake water obtained from a flow system in the laboratory and pumped from Lake Washington. Each aquarium had an active airstone and a charcoal filter (Dynaflow magnetic), and were on aquarium shelves with neon tubes (Gro-lux) suspended 22 cm. above. The photoperiod was kept at 14 hours of light each day. Newly hatched fry were fed crushed

TABLE 1

Means and variances for number of plates and gill rakers of male and female Gasterosteus, Lake Wapato, and tests of significance for differences in variance between sexes

		<i>N</i>	$\bar{X}$	<i>V</i>	<i>F</i>
Lateral plates (21° C.)	♂♂	463	14.80	9.61	1.17 (N.S.)
	♀♀	495	14.76	8.24	
Lateral plates (16° C.)	♂♂	617	16.26	26.01	1.16 (N.S.)
	♀♀	669	16.78	30.14	
Gill rakers (21° C.)	♂♂	245	18.93	3.53	1.11 (N.S.)
	♀♀	231	19.14	3.92	

infusoria tablets (Longlife). After 3 days they were fed nauplii of brine shrimp (Longlife) twice daily for 6 weeks, and thereafter were fed live tubifex worms.

Offspring of parents collected at Lake Wapato in the spring of 1968 were reared at room temperature. As measured by constant temperature recorders (Bristol Recording Thermometers) in aquaria this was 21 °C. $\pm$ 0.8 during the period of development of plates and gill rakers (up to 28 mm., see below). Offspring from Lake Wapato parents collected in 1969 were reared at 16° C. $\pm$ 0.5 by placing aquaria in large plastic troughs (2.5 m. long by 0.8 m. wide) filled with water. Water temperature in the troughs was controlled by refrigeration units (Min-O-Cool, Model D1-100, Frigid Units, Inc.). When fry reached a size of 28 mm. or more they were transferred to the aquarium shelves at room temperature, because number of plates and gill rakers are then fully developed. In 1970 parents were collected from the five populations mentioned, and their progeny were reared at room temperature (21° C. $\pm$ 0.8) like those from Lake Wapato. These temperatures are well within the range of those recorded at nests of males in the field.

Counts of gill rakers and plates were made according to the criteria of Hagen and Gilbertson (1972). All gill rakers on the first gill arch were counted, but on the left side only. Plates were counted on both sides of each individual and were summed between sides, so counts shown in the tables will in general be twice those usually given elsewhere.

Plate and raker counts were usually made on progeny when they had grown to sexual maturity, at about 7 months and a size of 35 to 44 mm. But in some instances individuals or entire families died of disease (*Ichthyophthirius*) or of unknown causes. To make counts reliably on such individuals we must know when development of the trait is complete. This is difficult to estimate for rakers as counts cannot be made on live fish. But progeny of about 25 mm. size have counts like those of their parents and there is no suggestion of missing or undeveloped rakers along the gill arch (sample of 388). Counts of plates were made on more than 600 live progeny when they had grown to 28 mm. by placing individuals on a moist cushion of cotton under a binocular dissecting scope. They were then quickly returned to their aquaria, and counts were repeated 4 months later at sexual maturity. The discrepancy in counts was less than 1 per cent. This error is about the same as the observational error we obtained from repeated counts on adults (Hagen and Gilbertson, 1973). Frequencies of the three plate morphs scored in a comparable sample showed no differences between fry and adults. So apparently development of plates and rakers is complete at a size of at least 28 mm. in these populations, and I restricted counts to individuals of 29 mm. or greater.

3. ANALYSIS AND DISCUSSION

Heritability (h^2) is defined in the "narrow" sense as the ratio of the additive genetic variance to the total phenotypic variance. This may be evaluated either by extracting variance components from the correlations among relatives or by regression (Falconer, 1960). With the large number of families available I have employed the regression method.

TABLE 2
Gill raker number for parents and offspring of Gasterosteus from Lake Wapato; offspring reared at 21° C. $\pm$ 0.8

Parents		Offspring			Number of offspring
♂	♀	♂♂	♀♀	Mean	
20	16	19.20	19.40	19.30	10
17	17	18.20	17.67	18.00	8
19	19	18.88	20.00	19.25	12
18	16	17.85	18.50	18.13	23
20	20	20.67	21.50	21.22	9
17	17	18.38	18.00	18.25	24
20	16	17.57	18.67	18.23	35
17	18	17.40	18.37	18.02	42
21	22	21.53	21.65	21.61	38
16	14	16.33	15.60	17.82	8
17	18	18.67	18.44	18.56	18
17	17	18.00	18.09	18.06	17
16	13	16.33	15.88	18.10	17
16	17	18.00	17.00	17.44	9
18	19	18.78	19.11	18.93	41
18	16	17.88	17.75	17.83	12
21	16	19.35	19.94	19.68	59
18	16	19.33	18.20	18.82	11
17	21	19.60	19.12	19.43	23
20	19	19.57	20.09	19.70	46
24	26	23.71	22.14	22.93	14

TABLE 3

Lateral plate number for parents and offspring of Gasterosteus from Lake Wapato; offspring reared at 21° C. ± 0.8 and 16° C.

At 21° C						At 16° C.					
Parents		Offspring			Number of offspring	Parents		Offspring			Number of offspring
♂	♀	♂♂	♀♀	Mean		♂	♀	♂♂	♀♀	Mean	
12	12	13.00	12.00	12.67	9	18	14	15.89	15.89	15.89	18
14	16	14.42	14.33	14.37	27	14	14	14.70	13.87	14.20	25
14	16	14.40	14.80	14.60	10	15	28	20.00	19.05	19.45	33
14	14	13.83	13.74	13.77	31	14	14	14.00	14.06	14.04	22
18	14	14.60	14.17	14.89	15	12	14	13.00	13.00	13.00	29
14	12	13.26	13.40	13.29	24	14	12	13.72	13.88	13.80	50
20	20	15.59	15.43	15.53	36	16	24	21.75	19.33	19.50	10
16	22	15.43	15.89	15.63	62	12	12	12.00	12.14	12.08	26
12	12	0.00	0.00	12.66	41	14	12	13.52	13.58	13.55	78
17	14	13.86	14.20	14.09	88	28	13	20.00	21.39	20.78	32
24	24	17.30	17.20	17.28	25	14	29	18.96	19.82	19.34	50
17	14	14.24	15.00	14.44	34	14	22	16.44	17.75	17.06	17
14	14	0.00	13.70	13.70	27	15	14	14.15	14.14	14.15	47
28	12	0.00	14.56	14.56	9	24	24	19.76	22.78	20.97	35
23	12	12.00	18.27	17.88	16	14	28	20.82	20.50	20.60	68
16	17	0.00	15.00	15.00	7	16	26	18.09	20.17	20.52	23
13	12	13.25	13.75	13.50	8	12	12	12.59	12.69	12.64	56
14	13	12.50	14.14	13.78	9	28	14	18.40	20.41	19.32	37
23	19	16.20	16.00	16.12	8	14	13	13.60	13.61	13.61	84
14	14	14.25	13.50	14.00	12	12	13	13.00	13.29	13.14	36
14	14	14.28	13.78	14.00	16	14	12	13.07	11.50	12.60	20
8	8	12.23	13.30	12.70	23	14	12	13.50	13.10	13.24	29
14	14	13.33	14.33	14.00	9	26	14	17.90	19.14	18.74	31
16	11	13.06	14.24	13.69	39	26	14	20.43	17.20	19.08	12
19	16	15.81	15.75	15.79	24	21	12	17.42	21.33	18.20	15
11	9	13.78	12.81	13.20	35	18	14	13.60	17.28	15.75	12
14	15	14.07	14.30	14.21	42	19	12	16.00	16.88	16.54	13
14	15	14.13	14.43	14.32	38	14	23	17.00	16.69	16.85	33
14	14	13.67	14.20	14.00	8	16	13	14.46	13.81	14.10	29
15	12	13.89	13.67	13.78	18	16	21	17.60	20.25	19.23	13
24	12	16.67	17.09	16.94	17	19	14	16.21	16.90	16.49	73
28	28	21.78	24.75	23.18	17	15	27	18.92	19.00	18.96	50
16	14	14.50	14.80	14.67	9	14	28	18.78	24.00	20.76	29
13	24	17.83	16.17	17.10	41	27	15	17.83	23.00	20.18	22
18	17	17.38	18.75	17.83	12	24	12	18.41	18.29	18.33	72
14	14	13.85	13.58	13.69	59	22	14	18.32	19.22	18.85	46
14	13	13.50	12.20	12.91	11	8	10	9.57	9.14	9.36	14
12	18	15.00	16.25	15.43	23						
16	13	15.63	16.64	15.87	46						
8	14	10.14	12.00	11.07	14						

Several points should be mentioned before discussing the heritability estimates. First, most of the parents were mated randomly as the number of plates and gill rakers were counted after the crosses were made. However, there are two sources of correlation between parents. Eight of the matings from Lake Wapato (four at each rearing temperature) were between parents deliberately chosen for extremes of high and low plate counts. These positive assortative matings were made to decrease the sampling error of the regression of offspring on midparent values. Another source of correlation comes from the parents collected from the other five populations. They will be more alike than randomly chosen ones because there are large

TABLE 4

*Lateral plate number for parents and offspring of *Gasterosteus* from five localities in Washington; offspring reared at 21° C. $\pm$ 0.8*

	Parents		Offspring			Number of offspring
	♂	♀	♂♂	♀♀	Mean	
Lake Quinault	19	16	14.92	17.60	16.41	27
	16	18	15.18	16.80	16.12	26
	19	14	16.26	17.32	16.83	41
	18	18	17.00	18.12	17.67	27
	16	15	15.00	16.17	15.88	16
	16	16	15.25	16.64	15.91	23
Samish River	10	8	8.67	9.24	8.95	42
	6	8	9.16	8.61	8.89	37
	12	10	11.54	10.53	11.00	28
	12	8	10.17	10.62	10.43	28
Scatter Creek	14	14	14.25	14.00	14.12	32
	14	12	14.00	13.82	13.89	19
	14	16	14.58	14.00	14.24	29
	14	14	13.94	14.17	14.07	42
Chinacum Creek	10	8	10.19	10.10	10.14	42
	12	10	11.22	11.36	11.30	23
Conner Creek	14	14	13.91	14.38	14.18	27
	14	12	14.00	13.45	13.67	18

differences in mean plate number among these populations. This correlation among parents will not affect the regression (Falconer, 1960).

Second, the regression of means of offspring on midparent will be a valid estimate of the heritability only if the variances for the traits are equal in the two sexes (Falconer, 1960), which they are for both plates and gill rakers (table 1). Third, in estimating heritability from regression the question of how to treat variable family sizes arises. Methods of weighting families are discussed by Reeve (1955), but all have certain difficulties. I have given equal weights to all families; that is, no weighting is used.

The basic data for parents and offspring are set out in table 2 for gill rakers and in tables 3 and 4 for lateral plates. The heritabilities, shown in table 5, all have regressions that differ significantly from zero. The heritability of plates for the Wapato stocks at 16° C. is considerably greater than that at 21° C.; the two regressions differ significantly ($F_{1,74} = 36.5$; $P < 0.001$). The heritability of plates obtained from the five populations and reared at 21° C. is close to the estimate for Lake Wapato at 16° C.

TABLE 5

*Heritabilities (h^2) for lateral plates and gill rakers of *Gasterosteus*, and results of analysis of variance testing for departure of the regressions from zero*

	(h^2)	Standard error	d.f.	F	P
Plates, Wapato (21° C.)	0.50	0.043	1,38	137	<0.001
Plates, Wapato (16° C.)	0.83	0.033	1,35	618	<0.001
Plates, among populations (21° C.)	0.84	0.039	1,16	466	<0.001
Gill rakers, Wapato (21° C.)	0.58	0.056	1,19	218	<0.001

TABLE 6

Regressions (b) of male and female offspring on midparent for lateral plates and gill rakers in Gasterosteus

		Number of families	<i>b</i>	Standard error	Confidence limits
Plates, Wapato (21° C.)	♂♂	37	0.45	0.053	0.342 ≤ <i>b</i> ≤ 0.560
	♀♀	39	0.52	0.057	0.290 ≤ <i>b</i> ≤ 0.750
Plates, Wapato (16° C.)	♂♂	36	0.75	0.046	0.654 ≤ <i>b</i> ≤ 0.842
	♀♀	37	0.92	0.062	0.794 ≤ <i>b</i> ≤ 1.046
Plates, among populations (21° C.)	♂♂	18	0.74	0.054	0.632 ≤ <i>b</i> ≤ 0.848
	♀♀	18	0.92	0.041	0.838 ≤ <i>b</i> ≤ 1.002
Gill rakers, Wapato (21° C.)	♂♂	21	0.60	0.068	0.465 ≤ <i>b</i> ≤ 0.737
	♀♀	21	0.46	0.105	0.247 ≤ <i>b</i> ≤ 0.668

There will be differences in gene frequency among populations and so we may expect the heritability obtained from the five populations to be greatest. When this estimate is compared with the heritability from Wapato at the same rearing temperature (21° C.), the estimate for the five populations is considerably greater.

The regression of male and female offspring on midparent gives an estimate of heritabilities for the sexes (table 6). The sexes do not differ significantly (*i.e.* both regression coefficients fall within the two confidence limits), with the exception of the regressions for plates at 16° C. for which the females have a significantly greater value ($P < 0.05$). But we may take the previous heritabilities, for the sexes combined, as representative since the difference between sexes at 16° C. is barely significant and the remaining values are not.

The male and female parents for most of the crosses differ in number of plates and rakers (tables 2, 3, 4) so the regression of offspring on the male and on the female parent can be used to detect maternal effects (table 7). For plates none of the regressions on the two parents differs significantly. For gill rakers the regressions on the two parents do differ ($P < 0.05$), but it is the regression on the male parent that has the greater coefficient. This suggests there are no maternal effects, which was upheld by an analysis of the means of offspring from reciprocal crosses (from tables 2, 3, 4).

The data also provide evidence on the heritability of asymmetry in plate number because about 37 per cent. of the parents differ in counts

TABLE 7

Regressions (b) of offspring on male and female parent for lateral plates and gill rakers in Gasterosteus

		Number of families	<i>b</i>	Standard error	Confidence limits
Plates, Wapato (21° C.)	♂	40	0.33	0.047	0.232 ≤ <i>b</i> ≤ 0.420
	♀	40	0.36	0.056	0.244 ≤ <i>b</i> ≤ 0.472
Plates, Wapato (16° C.)	♂	37	0.39	0.080	0.225 ≤ <i>b</i> ≤ 0.548
	♀	37	0.36	0.056	0.244 ≤ <i>b</i> ≤ 0.472
Plates, among populations (21° C.)	♂	18	0.79	0.071	0.648 ≤ <i>b</i> ≤ 0.932
	♀	18	0.75	0.069	0.612 ≤ <i>b</i> ≤ 0.888
Gill rakers, Wapato (21° C.)	♂	21	0.58	0.082	0.417 ≤ <i>b</i> ≤ 0.743
	♀	21	0.40	0.064	0.275 ≤ <i>b</i> ≤ 0.513

between sides. Matings between parents can be grouped into those with both parents symmetric, one parent asymmetric by one plate (a difference of one plate between sides), both parents asymmetric by one plate, and both parents asymmetric by more than one plate. The frequency of symmetric and asymmetric offspring in each group is then found. The difference is highly significant, asymmetric parents having a greater number of asymmetric progeny (table 8), which strongly suggests a rather large heritable component in asymmetry of plates. The estimation of heritabilities by regression is straightforward when the characters can be measured on a continuous scale, but this does not apply when the characters have a discontinuous distribution with an "all-or-none" classification. For example, nearly all the sticklebacks are symmetric for plate number, or they

TABLE 8
Lateral plates of Gasterosteus: number of symmetric and asymmetric offspring from parents with increasing degrees of asymmetry. Chi-square testing a difference in distribution of asymmetric offspring

Parents	Offspring	
	Symmetric	Asymmetric
Symmetric	992	163
Asymmetric for one plate (one parent)	631	247
Asymmetric for one plate (both parents)	49	66
Asymmetric for more than one plate (both parents)	100	40

$$\chi^2_{(3)} = 145.5 \quad P < 0.001.$$

are asymmetric with a difference of one plate between sides (table 8); the distribution is highly discontinuous. Falconer (1965, 1967) developed a method for estimating the heritability of characters having an "all-or-none" classification, and the method can be used to estimate the heritability of asymmetry. Since the parents are randomly sampled and randomly mated with respect to asymmetry of plates, the data required to estimate the heritability are the frequencies of symmetric and asymmetric progeny from the parents that are both symmetric, and those with one or both the parents asymmetric (table 8, with all asymmetric classes of parents grouped). Applying Method 2 of Falconer (1967; equation 4, pages 60 and 74) the heritability and standard error for asymmetry is 0.63 ± 0.16 . This is an estimate of the proportion of additive genetic variance.

There are significantly more female offspring and adults in Lake Wapato than there are males (Hagen and Gilbertson, 1973), and in the laboratory-reared offspring most clutches show a wide departure from an equal sex ratio although the overall ratio does not depart from equality (table 1). Lindsey (1962) gave evidence that temperature and density affected sex ratio in threespine sticklebacks. My clutches from Lake Wapato were reared at two temperatures and there are rather large differences in density among families, so I have analysed the data for effects of temperature and density

on sex ratio by analysis of covariance (table 9). The results give no evidence that temperature or density effect the sex ratio.

Heritabilities for lateral plates and gill rakers in Lake Wapato and for lateral plates in five other populations are high. How far can we generalise the results? Heritabilities are of course specific for particular populations and for a specified set of environmental conditions. But all parents were collected from the field where they would experience large fluctuations in the environment during development, and so increase the environmental variance of the phenotype. Nevertheless, heritabilities of their offspring reared in the laboratory are high, so we may have confidence that similar values exist in these populations.

As mentioned, there is evidence for strong natural selection in populations of sticklebacks, from predation acting on number of plates and from

TABLE 9

Analysis of covariance for effects of rearing temperature (21° C. and 16° C.) and density on sex ratio in Gasterosteus. The dependent variable is the fraction of the female offspring (arcsine transformed)

Source of variation	Total		Due to regression		Error	
	Degrees freedom	Sums squares	Degrees freedom	Mean square	Degrees freedom	Mean square
21° C.	38	2.7990	1	0.0503	37	0.0743
16° C.	36	0.4766	1	0.0158	35	0.0132
Within temperatures (pooled)	—	—	—	—	72	0.0446
Regression coefficient	—	—	—	—	1	0.0628
Common (21° and 16° C.)	74	3.2761	1	0.0032	73	0.0448
Adjusted means	—	—	—	—	1	0.0344
Total	75	3.3194	1	0.0121	74	0.0447

Effects of family size on sex ratio: 21° C. $F_{1,37} = 0.677$ (n.s.); 16° C. $F_{1,35} = 1.20$ (n.s.).

Effects of temperature on sex ratio: $F_{1,73} = 0.768$ (n.s.).

feeding specialisation on gill rakers. The results here point to a large store of additive genetic variance present in these populations that is available for response to selection. The large temporal and abrupt spatial changes we have found for these traits are most probably a result of selection, acting in part through the agents of predation and food source, on this genetic component.

In a classic study of asymmetry in *Drosophila melanogaster*, Mather (1953) showed that the asymmetry in number of sternopleural chaetae is under genetical control, which is probably polygenic, and he also showed that the level of asymmetry increased with inbreeding. Also Beardmore (Ph.D. Thesis, Sheffield, 1956) and Thoday (1958) showed that asymmetry for sternopleural chaetae in *Drosophila* increased with directional selection. The number of plates and gill rakers of sticklebacks in Lake Wapato have been under directional selection, which is almost certainly a result of a recent colonisation from Lake Chelan (Hagen and Gilbertson, 1973). The high heritability found here for asymmetry of plates may in fact be a result of strong directional selection acting on this trait in Wapato, since we may expect the additive variance to increase as gene frequency rises to intermediate values.

Acknowledgments.—I am indebted to Messrs David Semler, L. G. Gilbertson, and Miss Phyllis Drayton for their help in the field, and for their assistance with sticklebacks in the laboratory. Drs J. Felsenstein, P. O'Donald and Professors Bryan Clarke and C. C. Lindsey

made helpful suggestions on the manuscript; especially I thank Dr P. O'Donald for calling to my attention some important references. The research was made possible by a grant from the National Science Foundation (GB-7686).

4. REFERENCES

- BEARDMORE, J. A. 1956. Ph.D. Thesis. University of Sheffield.
- BERTIN, L. 1925. Recherches bionomiques, biometriques et systematiques sur les Epinoches (*Gasterosteides*). *Ann. Inst. Oceanograph. Monaco*, N.S., 2, fasc. 1.
- FALCONER, D. S. 1960. *Introduction to Quantitative Genetics*. Oliver and Boyd, Edinburgh and London.
- FALCONER, D. S. 1965. The inheritance of liability to certain diseases, estimated from the incidence among relatives. *Ann. Hum. Genet., Lond.*, 29, 51-76.
- FALCONER, D. S. 1967. The inheritance of liability to diseases with variable age of onset, with particular reference to diabetes mellitus. *Ann. Hum. Genet., Lond.*, 31, 1-20.
- HAGEN, D. W. 1967. Isolating mechanisms in threespine sticklebacks (*Gasterosteus*). *J. Fish. Res. Bd., Canada*, 24, 1637-1692.
- HAGEN, D. W., AND MCPHAIL, D. 1970. The species problem within *Gasterosteus aculeatus* on the Pacific coast of North America. *J. Fish. Res. Bd. Canada*, 27, 147-155.
- HAGEN, D. W., AND GILBERTSON, L. 1972. Geographic variation and environmental selection in *Gasterosteus aculeatus* L. in the Pacific Northwest, America. *Evolution*, 26, 32-51.
- HAGEN, D. W., AND GILBERTSON, L. 1973. Selective predation and the intensity of selection acting upon the lateral plates of threespine sticklebacks. *Heredity* (in press).
- HEUTS, M. J. 1947a. The phenotypic variability of *Gasterosteus aculeatus* L. populations in Belgium. *Meded. Kon. Vl. Akad. Wetensch.*, 25, 5-63.
- HEUTS, M. J. 1947b. Experimental studies on adaptive evolution in *Gasterosteus aculeatus* L. *Evolution*, 1, 89-102.
- HEUTS, M. J. 1956. Temperature adaptation in *Gasterosteus aculeatus* L. *Publ. della Stazione Zool. die Napoli*, 28, 44-61.
- HUBBS, C. L. 1929. The Atlantic American species of the fish genus *Gasterosteus*. *Occ. Pap. Mues. Zool., Michigan*, 20, 1-9.
- LINDSEY, C. C. 1962. Experimental study of meristic variation in a population of threespine sticklebacks, *Gasterosteus aculeatus*. *Canadian Jour. Zool.*, 40, 271-312.
- MATHER, K. 1953. Genetical control of stability in development. *Heredity*, 7, 297-336.
- MILLER, R., AND HUBBS, C. 1969. Systematics of *Gasterosteus aculeatus*, with particular reference to intergradation and introgression along the Pacific coast of North America; a commentary on a recent contribution. *Copeia*, 52-69.
- MOODIE, G. E. E. 1972. Predation, natural selection and adaptation in an unusual threespine stickleback. *Heredity*, 28, 155-168.
- MOODIE, G. E. E., MCPHAIL, D., AND HAGEN, D. 1973. Experimental demonstration of selective predation on *Gasterosteus aculeatus*.
- MUNZING, J. 1963. The evolution of variation and distribution patterns in European populations of the threespine stickleback, *Gasterosteus aculeatus*. *Evolution*, 17, 320-332.
- REEVE, E. C. R. 1955. The variance of the genetic correlation coefficient. *Biometrics*, 11, 357-374.
- THODAY, J. M. 1958. Homeostasis in a selection experiment. *Heredity*, 12, 401-415.