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Heritability of Thermal Resistance in the Guppy (*Poecilia reticulata*, Peters)—II

M S SHAH[1] and J A BEARDMORE
Department of Genetics, University College of Swansea, Singleton Park, Swansea SA2 8PP, UK

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Two strains of the guppy "Lowestoft" and the "Swansea" (*Poecilia reticulata*, Peters) were selected for high thermal tolerance. The temperature-time regime was maintained at 44°C for 8 min. Selection continued for 6 generations in the Lowestoft strain and for 5 generations in Swansea strain. The calculated realized heritabilities were 0.41 for the Lowestoft strain and 0.48 for the Swansea strain. The results indicate that thermal resistance is a polygenic character and could be useful in undertaking selection programmes for high thermal tolerance in species of commercial importance.

Key Words: Heritability, Liability, Threshold, *Poecilia reticulata*

Introduction

The ability to resist a certain range of temperature is an organism's innate biological property which is mediated by complex physiological and developmental processes. As such, an individual's or populational's thermal characteristic that enables it to adjust its metabolic activity over the entire range of habitat or environmental temperature is determined by its genetical make-up (Prosser 1973, Hazel & Prosser 1974, Hochachka & Somero 1973). Being so, temperature tolerance characteristic may bear some considerable economic importance in those cases where thermal tolerance of commercial species is concerned.

Thermal resistance is a threshold character. It differs from a classical quantitative character, in that, its mode of expression occurs in a discontinuous or all or none fashion. Thus in testing the effects of a thermal shock at certain higher temperature, some individuals die, others do not, thereby constituting two visible phenotypic class of effects. Apparently they do not seem to follow the rules of transmission of a continuously variable character, a careful analysis can soon show that they conform to the same rule of

[1]*Present address*: Freshwater Aquaculture Research Station, Fisheries Research Institute, Mymensingh, Bangladesh

inheritance as do the quantitative characters. To understand the mode of transmission of threshold characters it is imporant to understand the concept of liability, a concept that relates to the association of an underlying continuous genetic variation which gives rise to the expression of graded phenotypic effects in an individual (Falconer 1965, 1967, Pirchner 1969). Being so in its expression, it can be measured to be inherited in the same way as do the quantitative characters. In quantitative genetic studies, measurement of heritability is important as it tells about the portion of variance in the total phenotypic variation, which is actually offered by the genotype of the organism, and that is actually determinant of the outcome of any selection experiment (Falconer 1981). The usual techniques of the analysis of quantitative characters which are mainly based on variance and correlation analysis (Wright 1921) do not sharply apply in the case of threshold characters. For them there are special techniques and concepts (Wright 1934, 1943).

Materials and Methods

Two strains of long-established colour patterns of the guppy were used. They were obtained from populations maintained in the departmental laboratory.

Culture and Maintenance of Fish

Fishes were cultured in fibre glass tanks measuring $24'' \times 16'' \times 10''$ with a capacity of 35 litres of water. For better air circulation in the tanks biological filter bed was used, on top of which a two and a half inch thick gravel bed was laid. Temperature of water in the tanks was maintained at 25°C with the help of thermostat control under-water heater. A twelve hour dark-light regime was maintained in the room with the help of auto set time switches. The fishes were fed "Aquarian Tropical Fish Flakes" and "Aquarian Vegetable Flakes" twice daily. The two products were taken in equal amount, ground in to powder, and mixed well before feeding. A control population was maintained for both selected lines with the similar conditions of culture and maintenance.

Application of Heat Shock

Heat shock was applied to a random sample of 10–15 fishes of age 5 to 6 weeks in a 250ml beaker with 200ml of water of the selection tank. The beaker with the fish was then placed in the thermostatically controlled water bath raised at 44°C. and exposed at that temperature for 8 minutes. Immediately after the exposure the fishes were transferred to a recovery tank set up with same temperature and aeration conditions as that of the selection tank. The period of recovery was found to vary between the individual survivors. However, after 2 to 3 hours the percentage of survival was recorded. The standard length of surviving fishes was measured after anaesthetizing them by lppt dose of Benzocaine (Shah 1984).

Heritability of Liability

The concept of liability made it possible to measure the heritability of liability of threshold character (Falconer 1981). In threshold characters the resultant phenotypes depends upon the determinant threshold (Falconer 1981). In termperature selection where it is ended up with two phenotypic classes of effects i.e., survive and dead, a single threshold is operative here. As it is dealt here with mass selection, the phenotypic class of effect is expressed as proportion or percentage of individuals that do or do not survive and it is called incidence (used in the same way as prevalence in the context of human diseases). As variances vary according to the mean, it was not thought proper to express the incidence in percentage scale. Therefore, incidences were converted into mean liability by some scale transformation. For the methods of calculating liability and obtaining mean

liability the useful reference can be made to the Falconer (1981).

Calculation of Heritability

The heritability is a fraction of the variance that is due to additive genetic variance of a character (Narrow sense). Broadly speaking, the word heritability (h^2G) is equal to the ratio between the genotypic and phenotypic variance.

$$h^2G=\sigma^2G/\sigma^2ph$$

For the practical purposes of breeding, it is important to partition the genotypic variation into variation actually derived from genes with additive effect, thus

$$h^2=\sigma^2A/\sigma^2ph$$

Of the several methods of determining heritability in experiment with fish, realized heritability is one which is determined by the ratio between R, the response of selection and S, the selection differential. In threshold character selection, the reference for the method for obtaining mean liability and that of R (response in difference in mean liability) and S (selection differential) has been made in the previous section. Once these parameters are obtained the heritability of liability is obtained by regression of R on S with the regression equation $Y=\bar{Y}+b(X-\bar{X})$.

Results

The temperature-time regime of the experiment was primarily decided upon observing a

Table 1 *Data on parameters in the selected line of the Lowestoft strain of the guppy*

Generation	Temp. of expo. (°C)	Time of expo. (m)	No. of fish exposed	% of survival	Mean of SL of survivors (cm) (± S.E.)	Heritab (h^2) R/S
0	43	8	50	34.0	1.29±0 04	
1	,,	8	50	94.0		
1	44	,,	51	25.49	1.28±0.03	
2	,,	,,	38	28.49	1.29±0.04	
3	,,	,,	55	47.27	0.94±0.03	
4	,,	,,	58	48.28	1.03±0.02	
5	,,	,,	64	71.87	1.05±0.02	
6	,,	,,	50	80.0	0.94±0.01	0.41

Table 2 *Data on parameters in the selected line of the Swansea strain of the guppy*

Generation	Temp. of expo. (°C)	Time of expo. (m)	No. of fish exposed	% of survival	Mean of SL of survivors (cm) (± S.E.)	Heritab. (h^2) R/S
0	43	7	50	20.0	1.12±0.04	
1	,,	,,	40	80.0		
1	44	8	40	34.28	1.03±0.03	
2	,,	,,	52	39.0	0.93±0.02	
3	,,	,,	35	51.43	0.97±0.04	
4	,,	,,	34	67.65	0.97±0.03	
5	,,	,,	45	80.0	0.92±0.02	0.48

reasonable incidence of survival among exposed fishes. Initially the regimes were different for the two strains, one at 43°C for 8 min. and the other at 43°C for 7 min. Later, the regimes were both placed at 44°C for 8 min. because of high survival in the first generation. However, it is seen that in each generation the percentage of survival has increased gradually, though the Swansea strain had a faster response than that of the Lowestoft strain.

The size of the surviving fishes with respect to standard length was found to be related to the percentage survival in each generation. For both the strains, there is an apparent, though not very regular correlation between the two factors. The average size of the fishes gradually decreased in the later generations of selection, with increase of survival percentage.

The heritability values calculated for both the strains are shown in the tables 1 and 2. The values stand at 0·41 for the Lowestoft strain and 0·48 for the Swansea strain.

Discussions

The aim of the present experiment was to measure the heritability of thermal resistance in the guppy. The effect of thermal shock in fish has been discussed by Fry (1971). Bliss (1955) suggested the dose mortality method to measure the incipient lethal level of temperature and Fry (1971) also suggested the same method, in cases when the concept of a zone of resistance is not applied in assaying the lethality effects of temperature. In the present study, the incipent lethal level of temperature was measured in the same way by dosage mortality. However, the time of exposure is important because the time that a fish can resists the effects of lethal temperature shortens with the progressive rise of temperature until a point is reached at which the fish is killed instantaneously (Brett 1956). In the present experiment the temperature-time regime for both the strains were decided upon assaying that a reasonable incidence of survival can be attained at the regime in question. However, though the two regimes were initially fixed at 43°C for 8 minutes and 43°C for 7 minutes, they had to be shifted to a higher range, both being at 44°C for 8 minutes, because of an unprecedented high survival in the first generation. The explanation of this could most plausibly be made with the fact that as the sample used in the starting generation was derived from the large population tank with an apparently dense population they had had a lower survival. This factor could possibly be overcome by replacing fishes to a small tank, acclimatized there, and then using them in the starting generation but limited time and facilities had confronted the authors from doing that.

The uniform temperature-time combination at 44°C for 8 minutes for both the strains however, was found suitable to keep the intensity of selection at a moderate level where the survival percentage steadily increased in each generation. This increase was found to be related, though not on a very clearcut basis, with the gradual decrease of the size of the fishes with respect to standard length. Shah and Beardmore (in press) obtain similar relationship of the effect of temperature and size in some hybrid guppies. Ray (1960) has demonstrated that temperature can affect allozyme polymorphism and size of an organism. In *Balanus* sp., Nevo et al. (1977) obtained a strong effect of temperature on the allozyme polymorphism and size. The average size of the barnacles was found to be significantly decreased in the warmer canal than in the cooler canal.

The heritability values calculated stand at 0·41 for the Lowestoft strain and 0·48 for the Swansea strain. These values were obtained from the survival incidences on the concept of liability and have been shown in the from

of regression line in the figures 3 and 4. Kirpichnikov (1979) produced a comprehensive review on studies on the heritability of quantitative characters in fishes. A prior knowledge of heritability of any particular character is important because it tells about the portion of variability that is attributable to heredity in the total expression of the character. As for thermal resistance in fishes, great differences have been established in different groups of fishes. Ihssen (1973) obtained a heritability of 0·38 for thermal tolerance in the splake hybrid (*Salvelinus fontinalis* × *S. namaycush*), while Goddard and Tait (1976) reported thermal resistance as a polygenic character in the same fish with the evidence of effectiveness of selection after 4 generations of tests of temperature preference. In some hybrid guppies heritabilities for thermal tolerance were found to have a wide range of values with some positive relation with the level of genetic variability (Shah and Beardmore, in press).

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