An Age Factor Affecting Variance of a Behavioural Character in F_1 Hybrids Between Inbred Lines of the House Mouse

F_1 progeny of crosses between 2 inbred lines or species often show a greater variance of behavioural characters than the parental strains. This finding is at odds with what one would expect from studies on morphological characters (LERNER[1]). This puzzling feature has been discussed by CASPARI[2] and examples include TRYON's[3] well-known 'maze-bright' and 'maze-dull' rats, SCOTT's[4] findings relating to aggressiveness in 2 different breeds of dogs and HIRSCH's[5] work involving crosses between lines of *Drosophila* characterized by high and low levels of phototaxis. BROADHURST and JINKS[6] and MCCLEARN[7] have emphasized the need for appropriate scaling and in one particular instance the latter has shown, in a study of locomotor activity in the mouse, that a logarithmic tangent transformation of scores had the effect of equating P and F_1 variances and satisfying certain criteria for scalar adequacy. Nevertheless there exists, as yet, no reasonable biological explanation for this widely observed phenomenon.

In a study by one of us (G.A.v.O.) the behavioural characteristic 'fraying', displayed by mice during the building of (sleeping) nests, was examined in 2 inbred lines of mice and their hybrids. The fraying involved is the degree to which the smooth edges of standard strips of paper, 21 · 1 cm, are roughened or removed by the mice biting them when presented with strips for the first time. The strips were introduced into cages containing 1 mouse, were left there overnight, and removed the following morning. The animals were kept in small groups in cages with fine peat mould before and after testing. The parent strains used were CPB^{-s}, a Bagg Swiss and C57Bl/LiA; both highly inbred. The fraying characteristics of these strains are shown in Figure 1 and in the Table, clearly they differ strikingly in both mean and variance for the fraying character.

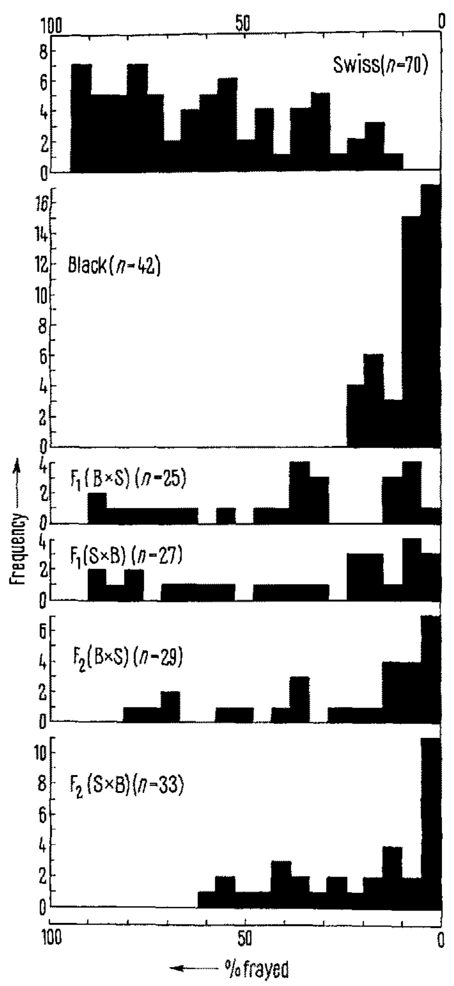

Fig. 1. The amount of fraying shown by 2 inbred mouse strains and their hybrids.

The variance shown by the reciprocal of F_1 (Table) is greater than that of the parental strains. Though these data are based upon several F_1 litters, interlitter variance is, as would be expected, of negligible size. Limited data on resultant F_2 crosses indicates that the variance is no greater than that in the F_1, a finding again common in studies in behavioural genetics.

A second series of tests using parents individually characterized by repeated testing and in which all F_1 progeny were scored at 3 months of age, revealed the situation shown in Figure 2. Here, despite the rather sparse data, it is clear that the F_1 progeny are not intermediate but resemble the C57Bl parent in their fraying behaviour. Further the interanimal variance is much lower than in Figure 1. Re-examination of the data summarized in this latter figure revealed that a considerable measure of heterogenity could be accounted for by differences in the age of the F_1 animals at the time of scoring. In Figure 3 the fraying score is plotted against the age at time of scoring for individual mice for each of the 2 reciprocal F_1. The lines shown are calculated regression lines; both regressions are highly significantly positive ($P < 0.01$ in both cases) and account for 62.9% and 34.7% of the total variance of the BxS F_1 and SxB F_1 respectively. The findings show that F_1 animals tend to resemble the C57Bl parent in early life changing in the course of becoming older to a behavioural phenotype closer to that of the Swiss parent.

Mean and variance for the fraying character in 2 inbred lines, their F_1 and F_2

	mean %	s^2 [a]
CPB^{-s} (S)	61.8	611.5
C57Bl (B)	5.7	32.6
F_1 (BxS)	39.0	889.8
F_1 (SxB)	36.3	978.5
F_2 (BxS)	23.1	672.4
F_2 (SxB)	19.0	387.8

[a] s^2 means the variance of the sample ($s^2 = [1/n - 1]\, \Sigma (x - \bar{x})^2$).

[1] I. M. LERNER, *Genetic Homeostasis* (Oliver and Boyd, Edinburgh 1954), p. 41, 56.
[2] E. CASPARI, in *Behaviour and Evolution* (Ed. A. ROE and G. G. SIMPSON; Yale Univ. Press, New Haven 1958), p. 118.
[3] R. C. TRYON, in *39th yearbook, Natn. Soc. for the study of Education*, (Ed. G. MONTROSE WHIPPLE; Public School Publ. Bloomington, Ill. 1940), p. 111.
[4] J. P. SCOTT, J. natn. Cancer Inst. *15*, 739 (1954).
[5] J. HIRSCH, in *Roots of Behavior* (Ed. E. L. BLISS; Harper and Brothers, Yew York 1962), p. 16.
[6] P. L. BROADHURST and J. L. JINKS, Psychol. Bull. *58*, 337 (1961).
[7] G. E. MCCLEARN, XIth Int. Conf. Genet. *3*, 795 (1963).

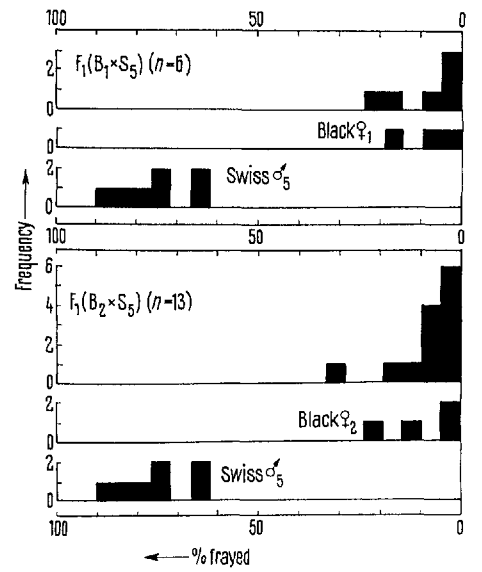

Figure. 2. The amount of fraying at 90 days of age of 2 nests of F_1 hybrids compared to the variability within each of the parents.

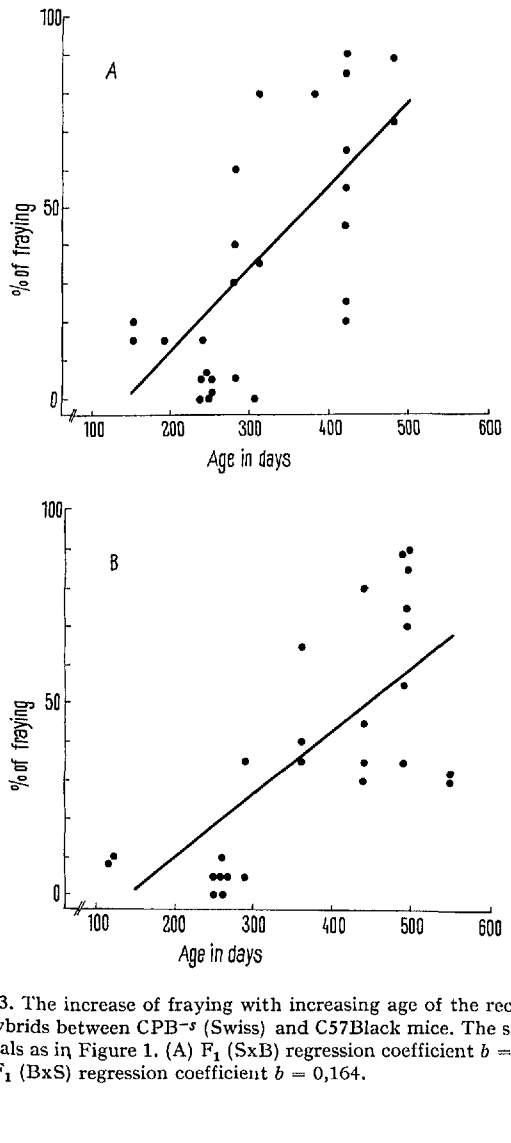

Fig. 3. The increase of fraying with increasing age of the reciprocal F_1 hybrids between CPB^{-s} (Swiss) and C57Black mice. The same F_1 animals as in Figure 1. (A) F_1 (SxB) regression coefficient $b = 0{,}223$; (B) F_1 (BxS) regression coefficient $b = 0{,}164$.

For mice from the parental strains, no relation between age and fraying score could be demonstrated statistically. Data so far accumulated from F_2 animals show a regression pattern which, though less steep, resembles that found in the F_1.

The genetic implications of these results are to suggest a change in regulatory mechanisms such that dominance and/or epistatic effects involving genes from the 2 haploid genomes making up F_1 zygotes are effectively reversed over a period considerably longer than the time taken by a mouse to reach maturity.

Dilger[8], in a study of nestbuilding in parrots of the genus *Agapornis*, concluded that interspecific hybrids, initially unsuccesful in nestbuilding attempts, learnt how to build from parental birds over a period of 3 years. Whilst this may be entirely correct, the possibility of a change in the hybrids similar to that found here cannot be excluded, since the initial behaviour resembled one of the parental species (*A. roseicollis*) whilst the later behaviour was similar to that of the second parent (*A. fischeri*).

The possibility of a learning process in the mice hybrids cannot be excluded absolutely but seems improbable since no mouse had experienced the presence of paper-strips or indeed any material other than fine peat before being tested. This possibility is, in any case, susceptible to experimental test as shown by Eibl-Eibesfeld[9] in his study of nestbuilding in the rat.

The data on the F_2 generation were gathered from animals in which the age distribution was not comparable with that of the F_1. It is therefore not possible at present to see in how far the expectation of greater variance due to segregation (after suitable correction for age) is fulfilled. There are, further, problems such as that of scaling (McClearn[7]) which are highly relevant but which await further investigation. The hypothesis of a temporal change in dominance or epistasis relations in hybrids is not, as such, a new phenomenon in genetics (Goldschmidt[10]) and certainly much further work is needed to analyse the genetic and physiological basis for behavioural characters. However, the observations presented here serve to suggest that attention might profitably be paid to the possibility of this or similar sources of variance being present in other work on behavioural genetics[11].

Zusammenfassung. Eines der Nestbauverhaltenselemente bei Mäusen (Beknappern von Papierstreifen) wurde bei 2 Inzuchtstämmen und deren F_1- und F_2 Hybriden verglichen. F_1-Tiere zeigten im Vergleich zu den Eltern eine grössere Variationsbreite des Verhaltenselementes. Ein grosser und besonders signifikanter Teil dieser Variabilität war einer altersabhängigen Verschiebung zuzuschreiben. Diese kommt wahrscheinlich nicht infolge eines Lernprozesses zustande, sondern durch Änderungen der genetisch-regulierenden Mechanismen (wie z.B. Dominanz und Epistasie).

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[10] R. Goldschmidt, *Physiological Genetics* (McGraw-Hill, New York 1938), p. 112.
[11] Research supported by a grant from the Netherlands Organization for the Advancement of Pure Research (Z.W.O.). The authors are grateful to Miss G. J. Blokzijl for help in making the German summary.