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Behavioural changes as a correlated response to selection

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Summary

Lines of mice have been selected for up to 50 generations on the following traits: high body weight, low body weight, high fat content or low fat content. The lines selected for high or low body weight differ by a factor of 2·5 and those selected for high or low fat content differ by a factor of five, both traits measured in 10 week old males. A set of behavioural traits was measured to ascertain whether this selection had caused correlated responses in behaviour: studies included feeding behaviour, open field behaviour, ultrasound calling rates of pups, and the response to the introduction of a novel physical object. Alterations in behavioural patterns which were expected *a priori* were observed but there appeared to be no changes in behaviour associated with any one selection criterion. Estimates of the genetic correlations between selected and behavioural traits were, with one exception, generally less than 0·1 in magnitude and not significantly different from zero (the exception was food intake in lines selected on body weight). Assuming that mice are accurate models for commercial species, then these results have important implications for animal welfare: they demonstrate that large scale behavioural changes do not arise as an inevitable consequence of intense long-term selection on traits of economic importance in commercial species.

1. Introduction

Species of commercial livestock such as chickens and pigs have undergone extended periods of intense artificial selection on characters such as growth rate and fat content. There is currently considerable concern about changes in the welfare of animals resulting from modern intensive agriculture methods: behavioural changes as a consequence of husbandry (such as battery rearing) have been investigated but to our knowledge no such investigation into the implications on behaviour of intense long-term selection on production traits has yet been attempted. For example, the pig industry incurs considerable economic loss due to aberrant behaviour such as sows neglecting their litters, or aggression between boars in transit. Pigs have been one of the most intensely selected commercial species for both increased body weight and reduced fat content but it is unknown whether these aberrant behaviours have been acerbated by the selection pressures or are solely a consequence of husbandry and inbreeding.

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There is also general interest in the evolutionary dynamics of behavioural traits (e.g. Boake (1994) and references therein). A common requirement of such evolutionary models is estimates of the genetic correlations between behavioural and physical traits such as body weight. Estimates from natural vertebrate populations are usually inferred from the resemblance between relatives and the present study complements this approach by providing estimates obtained from selection experiments.

This paper describes experiments on lines of mice subjected to long term selection on two physical traits: body weight and fat content. Mice are ideal subjects for this type of study as they may be selected rapidly on traits of interest (generation time can be as little as 9 weeks) and can be bred in sufficient quantities that a large number of observations can be made. Both factors are important given the high levels of variability typically observed in behavioural traits. Changes in behaviour will accumulate over many generations of selection and are more likely to be detected in this type of experiment than in protocols relying on comparison of relatives over a one- or two-generation interval. Importantly, selection can be

replicated, i.e. several independent lines can be derived from the same base population and selected on the same trait. A behavioural change present in all lines (replicates) selected on the same criterion is good evidence that it is a correlated response to selection rather than a spurious change associated with inbreeding or random genetic drift.

2. Materials and Methods

(i) *Mice*

Mice had been selected high and low for two traits of interest: body (protein) weight and fat content, known as the 'P' and 'F' lines respectively. There are therefore four types of lines: high body weight, low body weight, high fat content and low fat content. Their origins and responses up to generation 11 are described by Sharp *et al.* (1984). To summarize, they were derived from a cross between two inbred and an outbred line of mice and selected on the criteria of high/low body weight or fat content, selection being restricted to 10 week old males. There were three replicates within each of these four criteria giving 12 lines in total. At generation 20 several slight changes were made as described by Hastings, Yang & Hill (1991) and Beniwal *et al.* (1992*a*) the most important of which was that the three original replicates within each criterion were crossed to form a single replicate. The original replicates were numbered 1, 2 and 3 and the subsequent crosses as replicate 6 (as $1+2+3=6$); after crossing selection for high or low body weight was applied to both sexes while selection for high or low fat content continued to be applied only to males. The original replicates were maintained but selection was relaxed (discontinued). At the time of this experiment, the mice in replicates 6 had been selected for approximately 50 generations and differed 2·5 fold between the high and low body weight lines (50 g and 20 g respectively) and five fold between the fat and lean lines (20% fat and 4% fat respectively) when measured in 10 week old males. The high and low body weight lines differed in body weight but not fat content, while the fat and lean lines differed in fat content but not underlying lean (fat free) mass.

Mice were maintained at 23 ± 1 °C and provided with no. 1 food *ad libitum* except for gestating and lactating females which were provided with no. 3 food (food supplied by Beta Diets Ltd). Three types of cages were used: Large (500 mm × 250 mm × 110 mm) and small (290 mm × 110 mm × 110 mm) plastic cages which were constructed from 3 mm polythene and had an open grid lid (products number MB1 and MB23 from North Kent Plastics Ltd., Kent DA8 2AN, England) and metal cages (250 mm × 200 mm × 110 mm) constructed to a local design from 1 mm aluminium with a solid lid into which ventilation holes had been drilled. The metal cages and their effects on body composition are described in detail by Hastings & Hill (1993): mice born and raised in this type of cage had approximately twice the fat content of those reared in large plastic cages.

(ii) *Behavioural experiments*

Mice were examined at nominal ages (±1 week) of 5 weeks and 10 weeks. These ages represent times at which growth is maximal (5 weeks) or at which (chemical) maturity is achieved (10 weeks). Unless stated otherwise, all replicates were examined. The timing of experiments is given relative to the start of the dark period (e.g. -1 to $+2$ h).

Food intake and feeding behaviour

Animals were housed in same-sex pairs in small (MB23) plastic cages. Total food consumption over a five day period was measured by weighing the food hoppers at the start and end on this period. The feeding activity was estimated in each cage each day (3–6 h). Cages were observed every 30 s and individuals scored as one if feeding or zero if not feeding. The total feeding score was recorded over a 30 min period taken at random from within the 3–6 h time slot; this gives a reasonable estimate of the total time spent feeding and since each animal was scored every 30 s, their scores lie between 0 and 60. Individuals from the F6 line were subject to further investigation to compare feeding behaviour in the two types of cage. Mice were weaned into plastic or metal cages and, at ages 5–6 weeks, recorded on video over the period (-2 to $+10$ h) for two successive days. These periods were split into four time intervals (-2 to $+1$ h), (1–4 h), (4–7 h), (7–10 h); in subsequent statistical analysis (see later) these periods were fitted as fixed effects. The number of feeding bouts, their duration and hence the total time spent feeding were measured.

Ultrasound calling

Pup ultrasound calling facilitates communication between offspring and dam and is usually elicited by environmental stresses such as cold, isolation or hunger. It has been proposed as a general indicator of behavioural effects resulting from the pre-natal or immediate post-natal environment (in this case either direct genetic effects or maternal effects) (Zbinden, 1981; Rankin & Manning, 1993). The method used was as described by Rankin & Manning (1993). The litter was removed from its home cage and placed in a crystallizing dish lined with nesting material (dish A), and kept at 34–36 °C (a temperature comparable to that of the maternal nest) with a 25 W lamp. Each pup was individually removed from dish A and placed in a cooler dish (dish B, also lined with nesting

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material) kept at 24–26 °C; this acted as a mild thermal stress. Ultrasound emissions from each pup were measured using a QMC Instruments Mini-2 Bat detector set to detect frequencies of 70–80 kHz and mounted 10 cm above dish B. Scoring was delayed for 1 min after transfer to allow any reaction to handling to subside. After measurement, each pup was returned to dish A until the whole litter had been measured. Measurements were made on pups at 4, 5 and 6 days of age at time 3–6 h.

Open field behaviour and response to a novel object

The open field was a 400 mm × 400 mm square with 350 mm high walls; the floor was divided into 16 100 mm × 100 mm squares. The test animal was introduced into one corner and the number of squares crossed was recorded over the next 5 min; a square was considered as crossed if the subject placed one or more paws inside the box. In addition the total number of attempted escapes (defined as jumps at the wall where all four paws left the ground, defecation, urination and grooming bouts were counted in the following lines: FH3, FH6, FL6, PH1, PL1, PH6, PL1. At the end of this 5 min period a novel object (an irregularly shaped hollow orange plastic boot-shaped object with maximum height 75 mm, length 120 mm and width 60 mm) was introduced into the centre of the field. Three behavioural traits were recorded: time to first approach the object, time to first contact (with paw or nose) and time to full body contact; each subject had a maximum of 5 min to complete the test. If not completed (e.g. no body contact) the observation was scored as 'missing data' for subsequent statistics. The open field was cleaned with a mild disinfectant between tests which were performed at −1 to +2 hrs.

(iii) *Statistical analysis*

The results were analysed using the restricted maximum likelihood (REML) option of the Genstat statistical package (Genstat, 1988). When data are balanced (i.e. when all sub-groups have equal numbers of observations) the results are the same as those obtained by analysis of variance; in this case the data were unbalanced and REML is more appropriate as it weights correctly the comparisons between treatments (Patterson & Thompson, 1971). The following were fitted as fixed effects: (i) Selection criterion (i.e. large, small, fat & lean) (ii) Selection after generation 20 i.e. relaxed (replicates 1, 2, 3) or continued (replicate 6); this was cross-classified with criterion giving eight groups in total. (iii) Sex. (iv) Age, 5 or 10 weeks or age. (v) Cage type (plastic or metal). The following were fitted as random effects: (i) The effects of contemporaneity; for example fat replicate 1 and lean replicate 1 were tested at the same time and so on. (ii) The effects of individual lines: this accounts for the spurious genetic differences between lines which arise by inbreeding or genetic drift. (iii) Individual cage effects. Where repeated measures were made on the same mouse, individuals were fitted as a random effect. Some analyses required only a subset of these terms to be fitted: the model used in each analysis will be apparent in each table of results. The significance of differences between fixed effects was obtained by a *t*-test.

3. Results

The results are given on Tables 1–5. The most striking feature is the high levels of variability as measured by the coefficient of variation which typically ranges from 50% to 150% (discussed later). There were significant differences in food intake between the lines selected for high and low food intake (Table 1), and differences between the sexes in the frequency of urination in the open field (Table 3). Estimates of the genetic correlation r_a between the behavioural and selected traits are included in Tables 1–5; the method used to estimate r_a is described later.

Table 1. *REML analysis of feeding behaviour. P(H-L) is the difference between the high and low body weight lines, F(F-L) is the difference between fat and lean lines; sex, age and cage type are self-explanatory. Difference in mean food intake (g) over a 5 day period and feeding score over a 30 min period*

	Food intake	Feeding score
Line		
P(H-L)	22·65 ± 6·79*	1·8 ± 2·4
F(F-L)	4·88 ± 6·79	3·2 ± 2·4
Sex (female–male)	−2·80 ± 1·44	−0·7 ± 0·7
Age (5–10 weeks)	−1·70 ± 3·21	1·0 ± 1·7
Cage type (plastic–metal)	3·99 ± 3·53	n/a
N†	125	958
Mean	47·43	7·53
S.D.‡	6·16	7·7
CV†	13%	102%
r_a(P)§		
$h^2 = 0·3$	0·56 ± 0·17	0·04 ± 0·05
$h^2 = 0·1$	0·97 ± 0·29	0·06 ± 0·08
r_a(F)§		
$h^2 = 0·3$	0·09 ± 0·13	0·05 ± 0·04
$h^2 = 0·1$	0·16 ± 0·23	0·09 ± 0·06

† *N* is the total number of observations; for example each animal at each age in each time interval.
‡ S.D. taken as the square root of residual variance; *CV* = S.D./mean.
§ r_a(P) and r_a(F) are estimated genetic correlations between the behavioural trait and the selected trait in the P and F lines respectively, assuming the heritability of the behavioural trait (h^2) is either 0·3 or 0·1; see text for further details.
* $P < 0·05$; ** $P < 0·01$; *** $P < 0·001$.

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Table 2. *REML analysis of feeding behaviour in the F6 lines in different cage types. Number of feeding bouts over a 30 min period, average duration on these bouts (seconds), and the total time spent feeding. See legends on Table 1 for more details*

	Number	Mean duration	Total time
Line F(F-L)	−1·16 ± 3·48	39·3 ± 16·3	667 ± 311
Sex (female–male)	−2·28 ± 3·48	15·3 ± 16·3	37 ± 311
Cage type (plastic–metal)	0·23 ± 3·48	6·1 ± 16·2	222 ± 310
N	296	296	296
Mean	15·0	128·8	1979
S.D.	10·0	112·0	1867
CV	67%	87%	94%
r_a(F) $h^2 = 0{\cdot}3$	−0·01 ± 0·04	0·04 ± 0·02	0·04 ± 0·02
r_a(F) $h^2 = 0{\cdot}1$	−0·02 ± 0·07	0·07 ± 0·03	0·07 ± 0·03

Table 3. *REML analysis of open field behaviour. Activity (mean number of squares crossed per minute), number of defecation bouts (DB), urination bouts (UB), grooming (GB) bouts and number of attempted escapes (AE). See legends on Table 1 for more details*

	Activity	DB	UB	GB	AE
Line					
P(H-L)	0·5 ± 14·8	0·5 ± 0·4	0·24 ± 0·15	−0·1 ± 1·1	0·7 ± 1·0
F(F-L)	−6·5 ± 14·8	0·1 ± 0·4	−0·17 ± 0·15	0·2 ± 1·1	−0·2 ± 1·1
Sex (female–male)	−1·9 ± 4·0	−0·2 ± 0·3	−0·5 ± 0·1***	0·0 ± 0·1	0·8 ± 0·4
Age (5–10 weeks)	−16·7 ± 17·2	−0·4 ± 1·1	−0·3 ± 0·4	−0·5 ± 0·2*	0·7 ± 0·4
Cage type (plastic–metal)	−10·9 ± 10·4	−0·7 ± 0·6	−0·2 ± 0·2	0·0 ± 0·3	−0·3 ± 0·9
N	1062	774	774	774	774
Mean	150	3·5	0·58	1·63	1·51
S.D.	41	2·4	1·0	1·80	3·8
CV	27%	68%	172%	110%	252%
r_a(P)					
$h^2 = 0{\cdot}3$	0·00 ± 0·05	0·03 ± 0·03	0·04 ± 0·02	−0·01 ± 0·09	0·03 ± 0·0
$h^2 = 0{\cdot}1$	0·00 ± 0·10	0·05 ± 0·04	0·06 ± 0·04	−0·01 ± 0·16	0·05 ± 0·0
r_a(F)					
$h^2 = 0{\cdot}3$	−0·02 ± 0·04	0·00 ± 0·02	−0·02 ± 0·02	0·01 ± 0·07	−0·01 ± 0·0
$h^2 = 0{\cdot}1$	−0·03 ± 0·07	0·01 ± 0·03	−0·03 ± 0·03	0·02 ± 0·13	−0·01 ± 0·0

Table 4. *REML analysis of ultrasound calling (mean number of calls per pup per minute). See legends on Table 1 for more details*

Line	
P(H-L)	26·9 ± 26·6
F(F-L)	52·2 ± 26·6
Age	
4 days	97·3
5 days	127·4
6 days	135·3
S.E. of difference	9·0
Cage type (plastic–metal)	−81·8 ± 34·4
N	406
Mean	77
S.D.	70
CV	91%
r_a(P)	
$h^2 = 0{\cdot}3$	0·06 ± 0·06
$h^2 = 0{\cdot}1$	0·10 ± 0·10
r_a(F)	
$h^2 = 0{\cdot}3$	0·09 ± 0·05
$h^2 = 0{\cdot}1$	0·15 ± 0·08

4. Discussion

As expected the P high lines consumed considerably more food than the P low lines. The fat lines ate more than the lean lines but not significantly so. The high P lines are about three times the weight of the low lines and since maintenance costs are proportional to lean mass scaled to the power 0·75, then basal metabolic requirements of the high lines will be about $3^{0{\cdot}75}$ or approximately 2·3 times higher. The high lines also grow three times as fast so the food intake required for growth will also differ substantially. In contrast the fat and lean lines have identical underlying lean mass (Hastings & Hill, 1989, 1993) so maintenance requirements will be similar. Animals from the fat lines deposit on average an extra 1·2 g of fat over a one week period at ages 5 and 10 weeks compared to mice from the lean line (Hastings *et al.* 1991), equivalent to 0·86 g over a 5 day period. Energetic content of the food is 15·2 kJ/g (manufacturer's specification and it takes approximately 50 kJ to

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Table 5. *REML analysis of reaction to a novel stimulus. Time (seconds) to approach, make initial contact with, and make full contact with the novel object. See text for more details of the test and the legends on Table 1 for the key to table contents*

	Approach	Initial contact	Full contact
Line			
P(H-L)	2·2 ±11·4	7·7±23·5	−36·2±50·4
F(H-L)	0·22±11·4	11·6±23·5	50·1±50·4
Sex (female–male)	12·5 ±5·7	−3·6±15·5	120·0±66
Age (5–10 weeks)	19·6 ±7·4	22·6±27·5	23·8±25·7
Cage type (plastic–metal)	−21·7 ±13·8	52·2±42·3	−22·9±22·4
N	252	109	66
Mean	43·2	129	163
S.D.	43·9	61	57·6
CV	102%	47%	35%
r_a(P)			
$h^2 = 0·3$	0·01±0·04	0·02±0·06	−0·10±0·13
$h^2 = 0·1$	0·01±0·07	0·03±0·10	−0·16±0·23
r_a(F)			
$h^2 = 0·3$	0·00±0·03	0·02±0·05	0·10±0·10
$h^2 = 0·1$	0·00±0·05	0·04±0·08	0·18±0·18

deposit 1 g of triglyceride (HMSO 1974). This corresponds to an additional 2·8 g of food per mouse from the fat line or 5·6 g per pair and is in good agreement with the observed results of 4·9 g (Table 1). Both observations are therefore in line with prior expectations. Interestingly, the increased food intake in the high body weight line is not associated with a significantly increased feeding score. This implies that larger animals feed more effectively either by feeding more intensely or by virtue of their larger jaws (a scale effect), or by feeding more frequently in the light phase compared to mice from the low line, or a combination of all these factors. There was, however, a large CV in the feeding scores which makes putative changes difficult to detect. The data were skewed because many animals did not exhibit any feeding behaviour during some 30 min periods.

In the F6 lines, there was no difference in the number of feeding bouts but mice from the fat line spent more time feeding per bout, and hence spend a longer total time feeding (the results were just above the 5% significance level; Table 2). There was no apparent difference caused by cage type. In plastic cages, mice from the fat lines spent 24% of their time feeding and mice from the low line 15%; in metal cages the corresponding times were 19% and 15%.

None of the open field behavioural traits had altered significantly as a consequence of selection (Table 3), i.e. number of squares crossed (an indicator of activity), frequency of defecation or urination, frequency of grooming (an indicator of stress), or attempted escapes (usually an indicator of panic). There was a large and significant ($P < 0·001$) sex difference in the frequency of urination: males presumably using it for marking territory.

The lack of change in spontaneous activity as a consequence of selection on body weight appears to be in contrast to the belief, widely held among people working with lines selected on body weight, that mice from small lines tend to be more active. This observation dates from the first such experiments. For example MacArthur (1944) reported that mice from his Large line were 'sluggish' while mice from the Small line were 'active and aggressive'; similarly Falconer (1953) reported that mice from his Small line were more active than mice from the Large line which were 'slow and phlegmatic'. The activity reported by Falconer was reactivity to disturbance (i.e. opening the cage) when mice are likely to try and escape, and he showed that the successful escapees tended to be smaller (Falconer, 1989; p. 199). A subsequent study of these lines by Fowler (1962) found that spontaneous home-cage activity was if anything slightly lower in the Small line. These results suggest that the two behaviours are different traits rather than merely different manifestations of the same trait of 'activity', and under this assumption the apparent discrepancy disappears. There are also two further explanations: first, that the mice came from a different genetic stock from those of Falconer and MacArthur and therefore showed different patterns of correlated responses, or secondly, that the frequent handling of the mice over the course of the present experiment made them more docile and less likely to panic when placed in an open field.

Changes in ultrasound calling patterns may be a sign that conditions *in utero* have had an adverse effect on development (hence the use of ultrasound calling as an *in utero* toxicology test) or that environmental differences are present, for example differences in thermoregulatory capacities or hunger due to maternal

restriction of milk. No differences in calling rate appeared to be associated with the selection criteria (Table 4), and the expected (Rankin & Manning, 1993) increase in calling rate between days 4 and 6 was observed. This implies that large maternal effects had not occurred as a consequence of selection.

There were no apparent significant differences in the reaction to a novel stimulus (Table 5), which may be expected to indicate changes in the level of curiosity and fear.

Given the large phenotypic variance observed for the behavioural traits, there is obviously a huge potential for correlated changes in such traits to have occurred over the 50 generations of intense selection. High coefficients of variation (CV) were observed even after all fixed and random effects were removed by the models. Typically they were in the region of 50–150% and contrast strongly with variation in the morphological traits under selection, body weight and fat content, which typically have CVs of around 10–15%. The large CV of behavioural traits means that small changes as a consequence of selection would be undetectable against this background variation, even with the relatively large numbers of animals investigated. On a more positive note, it means that the large variation in behavioural traits appears not to have resulted in large correlated responses to selection. The correlated response (CR) in a behavioural trait due to selection on the selected trait is

$$CR = ih_s h_b r_a \sigma_{pb},$$

where

i is the intensity of selection of the selected trait (body weight or fat content); h_s is the square root of heritability of the selected trait; h_b is the square root of heritability of the behavioural trait; r_a is the genetic correlation between the two traits; σ_{pb} is the phenotypic S.D. of the behavioural trait (Falconer, 1989, p. 318).

It is more convenient to scale CR by its phenotypic standard deviation, giving:

$$\frac{CR}{\sigma_{pb}} = ih_s h_b r_a. \quad (1)$$

The known response in the F and P lines can be used to calculate the term ih_s from the equation $R = ih_s \sigma_a$ (where σ_a is the standard deviation of breeding value; Falconer 1989, p. 192) as follows (all values approximate). The P lines differ by 30 g with a phenotypic standard deviation of 4 g (data not shown). Heritability estimates in these lines lie in the region 0·4–0·5 (Sharp *et al.* 1984; Beniwal *et al.* 1992*a*, *b*) and are similar to those obtained in other experiments (Eisen, 1989). A value of 0·4 was assumed in the following calculations.

$$h^2 = \frac{\sigma_a^2}{\sigma_p^2}$$

so

$$\sigma_a = \sqrt{0{\cdot}4x4^2} = 2{\cdot}5\ g$$

and

$$ih_s = \frac{R}{\sigma_a} = \frac{30}{2{\cdot}5} = 12{\cdot}0.$$

The F lines differ by 20 percentage units (p.u.) of fat (24% *v.* 4%) with a phenotypic S.D. of 2 p.u. (data not shown). Heritability is again in the region 0·4–0·5 (Sharp *et al.* 1984; Hastings, 1989; unpublished). This is typical result (Eisen, 1989), and using the same procedure as above we obtain:

$$ih_s = \frac{R}{\sigma_a} = \frac{20}{1{\cdot}3} = 15{\cdot}4.$$

Previous studies on mice have concluded that significant heritabilities underlie many murine behavioural traits. Aggression, measured as the time taken for a resident male mouse to attack to an introduced 'intruder', has a realized heritability of 0·3 (Van Oortmerssen & Bakker, 1981), nest building behaviour a realized heritability of 0·3 (Lynch, 1980) and various learning traits had heritabilities lying between 0·2 and 0·5 (obtained as both realized heritabilities and by comparison of relatives; Wahlston, 1978). Also defecation rates in open field (usually taken as a measure of 'emotionality' (Hay, 1985, p. 13; Broadhurst, 1975) is heritable in rats (Broadhurst, 1975) and the behaviour of mice in open field experiments has a heritability of 0·26 (DeFries, Gervais & Thomas, 1978). If we assume a plausible value of $h_b^2 = 0{\cdot}3$ so that $h_b = 0{\cdot}5$ and substitute this value together with those obtained for ih_s into equation (1) then we can estimate the approximate magnitudes of r_a from the correlated responses ($CR/\sigma_{pb} = P$(H-L)/S.D. or F(F-L)/S.D.) which are given in Tables 1–5. The estimated magnitudes of r_a are small (less than 0·1) and do not differ significantly from zero (with the exception of food intake in lines selected on body weight). The heritability of the type of highly variable behavioural traits investigated here are likely to be less than those traits reported in the literature where presumably much effort has been invested in minimizing the environmental or stochastic variations in behavioural measurements. The analysis described above was repeated but assuming a heritability of behavioural traits of 0·1. The conclusions seem to be relatively robust: most estimates of r_a remained less than 0·1, and none were significantly different from zero. The exceptions were all in the *F* lines i.e. in food intake ($r_a = 0{\cdot}16$, Table 1), ultrasound calling rate ($r_a = 0{\cdot}15$, Table 4) and time to full body contact with the novel object ($r_a = 0{\cdot}18$, Table 5).

The overall impression after examination of these results is that selection was not associated with significant behavioural changes. Confidence in this

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conclusion is increased by the detection of those behavioural differences, such as food intake, which we knew to exist *a priori*, eliminating poor experimental procedure as an explanation for not observing differences, and by the low estimates of r_a. It was never the intention of this experiment to try and construct a type of 'psychological profile' of the mouse lines, rather the traits measured were chosen as general indicators capable of signalling changes in underlying behavioural patterns such as locomotor activity, curiosity, stress or aggression.

Given that this conclusion applies to mice, it is reasonable to consider its relevance to commercial species. Mammalian species have similar metabolism and the physiological and biochemical changes associated with response to selection appear similar in all species (including poultry). For example, the changes in fat metabolism caused by selection in the fat and lean lines were similar to those noted in chickens, pigs, cattle and sheep (e.g. Bannister *et al.* 1984; Muller, 1986; Asante *et al.* 1989; Hastings & Hill, 1990); changes in growth hormone levels as a consequence of selection for body weight in mice, sheep, pigs are similar; and so on. If we take the (reasonable) view that changes in behaviour are likely to be a consequence of hormonal and biochemical changes involved in the response to selection, the evidence from these mouse lines may be widely applicable: that response to intense long-term selection is not inevitably associated with significant changes in behaviour.

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