BOTH DIRECT AND INDIRECT GENETIC EFFECTS INFLUENCE BEHAVIOURAL RESPONSE IN MINK

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INTRODUCTION

Animal welfare is a major concern in modern production systems, and recently, a framework for their inclusion in breeding objectives was proposed (Olesen *et al.* 2000). Despite evidence that animal behaviour is genetically controlled and can be modified by selection (Malmkvist and Hansen 2001) the possibility of improving animal welfare by selection is not generally considered an option. For example, Nimon and Broom (1999) concluded that no positive effects of selection in mink could be expected on temperament and adaptation.
The behaviour of an animal is likely to be affected by both its own genotype, and by the phenotype and thus the genotype of its conspecifics (Moore *et al.* 1997), especially for traits, which are interactions between individuals. This results in interacting genotypes or indirect genetic effects (Moore *et al.* 1997), as an effect of the genotype of conspecifics on the phenotype of an animal. In mink conspecifics could be the dam and/or the other animal within a cage, as mink are normally reared two in a cage.
In this paper it is hypothesised that both direct and indirect genetic factors affect confident and fearful behavioural responses in mink. The hypothesis was tested by analysing a 12-year selection experiment for confident or fearful reaction towards humans.

MATERIAL AND METHODS

Selection lines. Three selection lines were initiated in 1987 from 150 female and 30 male mink of the black colour type. Mink kits were tested 3 times annually between September and November in a stick test. An observer placed in front of the cage introduced a wooden tongue spatula (stick) through the wire. The response was recorded as: (1) fearful if the mink escaped without touching the stick; (2) confident if the mink approaches and explores the stick; (3) aggressive if the mink attacks and bites the stick, and uncertain otherwise. Selection in each of the three lines was for increased frequency of each of these responses, selecting animals with the largest frequency of the response in repeated tests. The line selected for aggressive behaviour was stopped in 1991, due to reproductive problems. In 1992, an unselected control line was established by crossing the three lines. See Hansen (1996) for a complete description. In addition, from 1996 the mink were tested three times annually by Trapezov hand test (see Malmkvist 1996 for details). The hand test attempts handling the animal, with scores from –5 to +6, where negative scores indicate avoidance of, and positive scores interaction with a human. Two mink were kept in each cage and order of testing was not recorded. Generations were discrete and annual. A summary of the data from 1988 to 2000 is given in Table 1.

Statistical analyses. The following traits were analysed: *confident* and *fearful* behaviours measured as all-or-none responses in the stick test and the *Trapezov hand test* score (HT).
Data were analysed with a univariate linear animal model

$$Y = X\beta_0 + Z_1c + Z_2l + Z_3r + Z_4m + Z_5i + Z_6a + e$$

where Y is a vector of records, β a vector of fixed effects including a Year-Month-Sex subgroup and a regression on age at testing within YMC subgroups, c is a vector of random effect of cage ($N(0,I\sigma^2_c)$ with 4919 levels for confident/fearful and 1987 levels for the hand test), l is a random effect of litter environment ($N(0,I\sigma^2_l)$, 1700, 793), r is a random effect of environment common to repeated measures on an animal ($N(0,I\sigma^2_r)$, 8142, 3493), m is a random effect of maternal genotype ($N(0,A\sigma^2_m)$, i is a random effect of genotype of the other animal in the cage ($N(0,A\sigma^2_i)$), a is the additive genetic effect of animal ($N(0,A\sigma^2_a)$, 15234) and e is a vector of random residual ($N(0,I\sigma^2_e)$, 23397, 9063). Random effects were assumed to be uncorrelated, except for the three genetic effects, which was assumed to be multivariate normally distributed

$$\begin{bmatrix} a \\ m \\ i \end{bmatrix} \sim MVN(\begin{bmatrix} 0 \\ 0 \\ 0 \end{bmatrix}, \begin{bmatrix} \sigma_a^2 & \sigma_{am} & \sigma_{ai} \\ \sigma_{am} & \sigma_m^2 & \sigma_{mi} \\ \sigma_{ai} & \sigma_{mi} & \sigma_i^2 \end{bmatrix} \otimes A)$$

where A is the numerator relationship matrix for the 15234 animals tested and their ancestors. Variance components was estimated by an AI-REML algorithm (Jensen et al. 1997) implemented in the DMU package (Madsen and Jensen 2000).
Thus an indirect genetic effect of the dam is modelled, indicating that the genotype of the dam influences the behaviour of her kits. In addition, an indirect genetic effect of the cage mate is modelled, representing an effect of the genotype of the other animal in the cage.
The phenotypic variance was computed assuming that animals within a cage were unrelated. The relative importance of random effects is presented as the proportion of the phenotypic variance explained by that effect.

RESULTS AND DISCUSSION

Confident and fearful reactions were the most prevalent, as they accounted for 95% of the responses (Table 1). Aggression and uncertain responses accounted for less than 5% of responses.
The random effects of cage and common litter environment in total explained 1% to 5% of the variation. This is in agreement with cross-fostering experiments, showing no effect of the behaviour of the dam rearing the kits, but only an effect of the behaviour of the biological dam (Malmkvist and Hansen 2001). The environmental effects affecting repeated measures on the same animal accounted for 6% to 22% of the variation.
The direct heritability, the relative effect of the genotype of the measured animal accounted for 21% to 29% of the variation. The genotype of the dam explained 2% of the variation in confident and fearful responses, and 12% of the variation in the hand test score. The indirect genetic effect of the cage mate accounted for 3% to 4% of the total variation. Thus, indirect genetic effects explain a significant proportion of the variation.

Table 1. Mean and standard deviation of confident and fearful behaviours and the hand test score, number of observations, phenotypic variance and the proportion of the phenotypic variance explained by additive genetic (h^2_a), maternal genetic (h^2_m), indirect genetic of cage mate (h^2_i), cage (c^2), common litter environment (l^2) and environment common to repeated measures (r^2)

	Confident	Fearful	Hand test
Mean ± std	0.43 ± 0.49	0.52 ± 0.50	-0.06 ± 3.02
Observations	23397	23397	9063
Phenotypic variance	0.1612	0.1512	1.8250
h^2_a	0.208 ± 0.025	0.219 ± 0.026	0.287 ± 0.051
h^2_m	0.021 ± 0.010	0.023 ± 0.010	0.118 ± 0.034
h^2_i	0.044 ± 0.012	0.031 ± 0.011	0.033 ± 0.014
c^2	0.000 ± 0.017	0.000 ± 0.016	0.035 ± 0.024
l^2	0.010 ± 0.007	0.012 ± 0.007	0.012 ± 0.018
r^2	0.189 ± 0.033	0.223 ± 0.032	0.064 ± 0.040

The genetic correlations between direct and indirect genetic effects are shown in Table 2. Large positive correlations are found between the two indirect genetic effects, maternal genetic and cage mate genetic, for confident and fearful response. This indicates that for these traits, the indirect genetic effects of dam and cage mate are genetically the same trait. Negative correlations are found between direct and indirect genetic effects, except for the correlation between cage mate and direct genetic effects on the hand test score. For confident and fearful response, this indicates an antagonism, such that genetically confident or fearful animals tend to have a negative impact on the frequency of the same behaviour in their kits or cage mate. In contrast, for the hand test score, the effect of cage mate is not significantly genetically correlated to the other genetic effects.

Table 2. Genetic correlations between direct genetic, maternal genetic, and cage mate genetic effects for confident and fearful behaviours, and hand test score.

	Test	Direct	Maternal
Maternal	Confident	-0.64 ± 0.12	
	Fearful	-0.58 ± 0.12	
	Hand test score	-0.45 ± 0.11	
Cage mate	Confident	-0.53 ± 0.07	0.81 ± 0.24
	Fearful	-0.55 ± 0.10	0.99 ± 0.27
	Hand test score	0.14 ± 0.21	0.02 ± 0.24

The observed response in the selection experiment has resulted in a general reduction of fear in the confident line, measured in six different fear-eliciting situations, including a novel object, a human, an unfamiliar mink, unknown food, and a novel environment (Malmkvist and Hansen 2002). In addition, a correlated change in mating willingness was observed, with the confident line mating earlier than the fearful and control line (Malmkvist *et al.* 1997). The selection has

resulted in changes in the physiological response to acute stressors (Malmkvist 2001), indicating that selection caused not only a change in the observed behaviour, but also in the minks perception of stressors.
Confident and fearful behaviours were recorded as all-or-none responses. However, the model used has assumed normality. This is clearly not the case for all-or-none measures, and the assumption of homogenous variance is questionable. It is recommended that the present data be analysed with a threshold model with the same underlying model as presented here.
The model and results presented shows that the complex environmental and genetic interactions in behavioural reactions can be modelled and add to our understanding of the complexity of direct and indirect genetic effects as well as environmental effects on animal behaviour.
Indirect genetic effects may result in different predictions of evolutionary or selective potential (Moore *et al.* 1997), as part of the environmental effects affecting the phenotype of an animal is genetic. Thus, not only the genotype of the animal can change but also the environmental effects can evolve. In this study, indirect effects of dam and cage mate were considered. Potentially there could also exist indirect genetic effects of littermates and animals in neighbouring cages.

CONCLUSION

Both direct and indirect genetic effects, in addition to environmental effects, potentially influence the complex behavioural response of minks towards humans. It was shown that these effects can be modelled to increase our understanding of animal behaviour and welfare.
Confident and fearful responses to a stick test and hand test scores are influenced by both direct and indirect genetic effects, where indirect genetic effects are effects of the genotypes of the dam and the cage mate. For confident and fearful response, an antagonism between direct and indirect genetic effects was found. The presence of indirect genetic effects means that not only the genotype of the animal can evolve but also the environment that an animal experiences can evolve, as it is partly genetic.

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