Selection for temperament has no negative consequences on important production traits in farmed mink¹

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ABSTRACT: Danish and European legislation recommend mink breeding programs that include selection for “confidence,” defined as exploratory activity in a standardized behavioral test. Although this recommendation may improve mink welfare, farmers may consider this criterion risky due to possible negative consequences on other traits. The overall objectives of this study were to estimate the heritability of exploratory/fearful behavior and to identify genetic correlations with other traits of major economic importance in mink fur production. Various aspects of social influence on exploratory/fearful behavior, such as effects of the mother and litter siblings before weaning, the mother’s age, and cage mates after weaning, were analyzed. In total, 26,371 1-yr-old Brown mink (*Neovison vison*) individuals born during the period of 2013 to 2016 were included in the study. Exploratory/fearful behavior was the main trait analyzed. The production traits analyzed were live pelt quality and body weight. Both of these traits were assessed during live grading in November. Pelt length and

quality were determined using the dried pelts of nonbreeders. Fertility data were obtained from the Fur Farm database. Linear mixed models were run using the restricted maximum-likelihood method. The genetic correlation between female and male behavior was 0.95 (SE = 0.06), indicating similar genetic backgrounds for both sexes ($P = 0.40$). For both sexes, the estimated heritability of behavior was 0.19 (SE = 0.03). We found no significant genetic correlation between behavior and production/fertility traits ($P > 0.05$). Common litter variance indicated a preweaning effect of litter mates and/or dam on postweaning temperament. There was a tendency for offspring from older mothers to explore more than offspring from 1-yr-old mothers. This trend was especially pronounced for males of 2-yr-old mothers ($P = 0.05$) and females of 4-yr-old mothers ($P = 0.06$). We conclude that confidence may be selected for among farm mink without detrimental effects on economically important production traits, such as pelt quality and fertility.

Key words: correlated response, fertility traits, *Neovison vison*, pelt quality traits, social interaction, variance components

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INTRODUCTION

Mink have been kept in production systems for more than a century (Shackelford 1949, 1984; Enders 1952). Farm mink are bred for their fur. The most important production traits are high pelt quality, large pelt size, and high fertility (large litter size, decreased barrenness, and high survival rate among offspring). These traits are

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under intense selection in most breeding programs. However, the low frequency of handling during the lifetime of a mink and the preponderance of large production systems with more than 2,000 breeding females (Statistics Denmark, 2019) leaves little room for fear reaction dampening and taming through individual handling. The degree of domestication in the production of mink has been debated, and improvement of welfare is considered an important goal in the ethics of animal farming (European Commission, 2001). According to Danish legislation (Ministry of Food, Agriculture and Fisheries, 2006) and European recommendations (European Commission, 2001), breeding programs for mink production should include selection for confidence. The objective of the legislation is to increase animal welfare by selecting for domesticated, well-adapted mink that are less fearful.

Low levels of fearfulness and increased exploratory behavior (e.g., towards humans) are desired characteristics for a domestic phenotype with improved welfare (Malmkvist and Hansen, 2001; Price, 2002, 2008). However, production traits can have an antagonistic effect on other traits (Koivula et al., 2010), such that exclusive selection for one trait may lead to negative effects on another trait (Heringstad, 2003). Domestication has been suggested to induce morphological and physiological changes due to destabilizing selection (Belyaev, 1978). The degree to which selection for more confident mink will affect important production traits remains to be determined. If increased confidence is negatively associated with the most economically important production traits (e.g., pelt quality), deselection of fearful mink will be more difficult to implement in existing breeding programs.

The tendency toward confident versus fearful behavior in mink has been relatively well studied (Malmkvist and Hansen, 2002). The hereditary background for confidence has been documented in studies based on long-term selection experiments. The results of these experiments showed that behavior could be modified by selection. Selection for fearful mink resulted in a larger proportion of fearful mink; conversely, selection for confident mink decreased fearfulness in farmed mink (Hansen, 1996; Malmkvist and Hansen, 2001). Berg et al. (2002) found heritabilities of 0.21 and 0.22 for confident and fearful behavior, respectively.

In this study, voluntary approach/avoidance behavior was used as an index for temperament. The voluntary approach/avoidance test is the best validated test for evaluation of fearful/confident temperament (Malmkvist and Hansen, 2002). The

test has been used in the context of large-scale commercial mink production (Hansen and Møller, 2001) as well for ongoing welfare assessment of mink farms in all mink-producing European countries (Møller et al., 2015).

In previous studies of a mink line selected for confident behavior, males explored more than females on the stick test (Hansen, 1996; Malmkvist and Hansen, 2002). Behavior is both a product and a determinant of social interaction. It may be influenced by early life history, such as the effect of mother and litter mates before weaning. Postweaning interactions with family members versus strangers and with male versus female cage mates may also affect behavior (Alemu et al., 2016). Early life history and quality of maternal care may also influence fearfulness, as demonstrated in rats (Francis et al., 1999). However, these factors have not been investigated in mink.

The overall objectives of this study were to estimate the heritability of exploratory/fearful behavior in mink, using a simple approach-avoidance test, and to identify any genetic correlation between behavior and economically important production traits, such as pelt quality, BW, and fertility. We also investigated the effect of social environment on behavioral responses in farmed mink.

MATERIALS AND METHODS

Animals

In total, 26,371 brown mink (*Neovison vison*) born and raised at Foulum Research Farm, Aarhus University, Denmark, were used. The pedigree file, extracted from the Fur Farm database held by the Danish Fur Breeders Association, included 29,212 brown mink from up to 10 generations. Individuals for which data were available were traced for an average of 6.0 ± 2.6 SD generations.

The mink were exposed to natural lighting and housed in wire cages, in accordance with Danish legislation for mink production (Ministry of Food, Agriculture and Fisheries, 2015) (Hedensted-Gruppen, DK-8722 Hedensted, Denmark; W: 30 cm, H: 45 cm, L: 90 cm). Each wire cage was connected to a wooden nest box with a wire-mesh lid (W: 23 cm, H: 18.5 cm, L: 30 cm). The animals had permanent access to chopped barley straw on the nest box lid (mesh size: 2.5×2.5 cm). Each cage was equipped with a shelf (one wire tube cylinder (I: 32 cm, diameter: 11 cm) fixed to the cage ceiling). After separation from the dam at ~8 weeks of age (in July), one male and one female growing mink

were housed together in a single cage. As in standard production systems, sibs were primarily housed together. However, because of an excess of one sex in some litters, the kits from those litters were caged with nonsiblings. In some cases, a single cage housed two males or two females. The mink were fed ad libitum with a standard diet, from weaning to pelting. A total of 17,790 mink from this study were pelted in November, following Danish legislation for mink production.

Phenotypes

Mink born in three successive years (2014, 2015, and 2016) were subjected to the stick test described by Malmkvist and Hansen (2001; 2002). The animals were tested in November in their first year of life. Their responses were categorized in a standardized setting in their home cages for 15 s. Temperament was classified into four categories: “explorative” if the mink sniffed the stick persistently; “fearful” if the mink escaped/showed other fear responses and did not approach the test stimulus; “aggressive” if the mink attacked, bit/pulled the stick; or “indecisive” if the mink showed unclear or a mixture of approach–avoidance responses. Typically, during exploratory contact, minks sniffed and nudged the test spatula with their muzzles; sometimes they engaged in oral investigation with or without gentle biting. In aggressive contact, minks attacked the spatula intensively, with forceful biting and pulling of the spatula, often combined with agitated hisses. Because few animals were categorized as indecisive or aggressive, these two categories were excluded from the analysis, and we were left with “fearful” (score = 1) and “explorative” (score = 2). Female and male behavior was

analyzed separately because we expect that females and males may show different biologically determined thresholds for approach/avoidance behavior. Trait means are reported with SDs and the numbers of animals analyzed for each trait is reported in Table 1.

Mink born in the years 2013 to 2016 were evaluated for fur quality by live grading in November in their first year of life. Fur quality was scored in five categories, from category 1 (worst) to category 5 (best). The mink’s upper body was fixed in a tube on a grading table during live grading. A scale registered BW in grams automatically, and the weight values were transferred to a database stored in a computer. After pelting, measurements of pelt quality and pelt length were obtained from dried pelts prepared for auction from mink that were not selected for breeding. Pelt quality was scored in 12 categories, ranging from 1 (worst) to 12 (best). Pelt length was measured (in cm) from the tip of the snout to the tail joint and traits related to body size were considered separately for males and females. We employed the standard approach to evaluate pelt quality used in production mink (for a more thorough description of pelt quality traits, see Thirstrup et al., 2016).

Fertility data based on the litter of 1-yr-old females born between 2013 and 2015 were extracted from the Fur Farm database. Litter size was considered a trait of females and measured at approximately day 3 (first counting) and day 21 (second counting) after birth, at the same time as sex sorting. Information about the number of barren females and the percentage of surviving offspring were extracted from these data. Female mink that were mated, but did not deliver offspring, were classified as barren. Percent survival was calculated as

Table 1. Number of observations (N), mean, variance components¹, heritability (h^2), and effect of common litter (c^2) for all traits

Trait	N	Mean (SD)	σ_a^2 (SE)	σ_c^2 (SE)	σ_e^2 (SE)	σ_p^2 (SE)	h^2 (SE)	c^2 (SE)
Female behavior	7,386	1.32 (0.46)	0.038 (0.005)	0.011 (0.003)	0.154 (0.004)	0.203 (0.004)	0.19 (0.03)	0.06 (0.01)
Male behavior	7,094	1.48 (0.50)	0.046 (0.007)	0.012 (0.003)	0.178 (0.005)	0.236 (0.004)	0.19 (0.03)	0.056 (0.01)
Live pelt quality	20,230	3.45 (0.76)	0.18 (0.01)	0.03 (0.003)	0.32 (0.01)	0.53 (0.01)	0.35 (0.02)	0.05 (0.01)
Pelt quality	15,340	6.77 (2.30)	1.60 (0.14)	0.18 (0.04)	3.47 (0.09)	5.25 (0.07)	0.31 (0.02)	0.03 (0.01)
Female weight	10,248	2,032 (310)	51,381 (3,082)	9,943 (955)	29,485 (1,694)	90,810 (1,777)	0.57 (0.03)	0.11 (0.01)
Male weight	10,050	3,877 (549)	141,812 (11,085)	37,799 (3,574)	102,003 (6,036)	281,600 (5,614)	0.50 (0.03)	0.13 (0.01)
Female pelt length	7,231	76.86 (4.50)	8.86 (0.89)	2.26 (0.32)	6.88 (0.50)	17.99 (0.40)	0.49 (0.04)	0.13 (0.02)
Male pelt length	7,987	96.61 (5.28)	14.02 (1.25)	2.538 (0.411)	10.10 (0.72)	26.66 (0.57)	0.53 (0.04)	0.10 (0.02)
Barren	2,423	1.14 (0.35)	0.010 (0.005)	0.0004 (0.003)	0.11 (0.005)	0.12 (0.003)	0.08 (0.04)	0.004 (0.03)
First count	2,088	6.20 (2.72)	0.70 (0.31)	0.28 (0.22)	6.35 (0.31)	7.33 (0.23)	0.10 (0.04)	0.04 (0.03)
Second count	2,088	5.54 (2.80)	0.76 (0.32)	0.18 (0.23)	6.77 (0.32)	7.71 (0.25)	0.10 (0.04)	0.02 (0.03)
Survival	2,015	88.35(22.69)	45.87 (22.21)	17.57(16.40)	449.87 (22.47)	513.31 (16.59)	0.09 (0.04)	0.03 (0.03)

¹ σ_a^2 is the additive genetic variance, σ_c^2 is the common litter variance, σ_e^2 is the residual variance, and σ_p^2 is the phenotypic variance.

the percentage of offspring in a litter that survived from the first to the second counting (from day 3 to day 21 postpartum).

Histograms of trait distributions (Figures 1–11) indicated no substantial deviation from normality for the quality traits, BW (in g), body length (in cm), and first and second count of kits, indicating that the use of linear models would be acceptable. Although behavior and barrenness are binary traits on the observable scale, and survival is the difference between first and second count, we analyzed all traits using a linear model. For all traits, we only had one observation on each animal and we had convergence problems when we tried to use generalized linear mixed models. In the histograms, BW frequency was summed over 500-g intervals for males and 200-g intervals for females. Body size frequency was summed over 5-cm intervals for males and 4-cm intervals for females. For kit survival, frequency was summed over 10% intervals. Interval means are provided on histogram x axes.

Statistical Tests

Linear mixed models were run using the restricted maximum-likelihood (REML) method, as implemented in DMU software (Madsen et al., 2014). Due to problems with convergence in multiple-trait models, traits were analyzed using linear mixed bivariate animal models. The animal model used for the analysis was:

$$y_i = Xb_i + Za_i + Wc_i + e_i,$$

where y_i is a vector of observations for trait i ($i = 1, 2$), b_i is a vector of fixed effect, and a_i , c_i , and e_i are vectors of random animal, common litter, and residual effects, respectively. The matrices X , W , and Z are the incidence matrixes relating y_i to b_i , a_i , and c_i .

A separate model was used to analyze each trait. The fixed effects included in behavioral analyses were effect of house-year (36 levels, 3 yr, and 20 different houses after weaning), mother's age (four

Figure 1. Frequency distributions of male and female behavior scores.

Figure 2. Frequency distribution of live quality scores.

Figure 3. Frequency distribution of pelt quality scores.

levels: 1 to 4 yr old), and cage mate (four levels: with an opposite-sex sibling, opposite-sex nonsibling, same-sex sibling, or same-sex nonsibling). For pelt quality and body size traits, fixed effect of house-year (36 levels) was included. The fixed effect of sex (male or female) was included in the model for pelt quality traits. For fertility, fixed effect house-year was included. Random additive genetic effects of animal (a), common litter (c), and residual (e) factors were assumed to be independent and normally distributed, as follows:

$$\begin{bmatrix} a \\ c \\ e \end{bmatrix} \sim \left(\begin{bmatrix} 0 \\ 0 \\ 0 \end{bmatrix}, \begin{bmatrix} G_0 \otimes A & 0 & 0 \\ 0 & C_0 \otimes I & 0 \\ 0 & 0 & R_0 \otimes I \end{bmatrix} \right)$$

where $a = \begin{bmatrix} a_1 \\ a_2 \end{bmatrix}$, $c = \begin{bmatrix} c_1 \\ c_2 \end{bmatrix}$, and $e = \begin{bmatrix} e_1 \\ e_2 \end{bmatrix}$, A is the numerator relationship matrix, and I is the identity matrix. G_0 and C_0 are the additive genetic and common litter co-variance matrices, respectively, and R_0 is the residual co-variance matrix. $\otimes$ represents the Kronecker product.

Variance components [additive genetic variance (σ_a^2), common litter variance (σ_c^2), residual variance (σ_e^2), and phenotypic variance (σ_p^2)] were estimated. For each trait, heritability and the effect of common litter were calculated from estimated variance components. Estimates of heritability were calculated as $h^2 = \sigma_a^2 / (\sigma_a^2 + \sigma_c^2 + \sigma_e^2)$. Estimates of common litter variance were calculated as $c^2 = \sigma_c^2 / (\sigma_a^2 + \sigma_c^2 + \sigma_e^2)$. Genetic and phenotypic correlations, as well as correlations due to common litter, were estimated for male vs. female behavior and for behavior vs. pelt

Figure 4. Frequency distribution of female weight summed over 200 g intervals.

Figure 5. Frequency distribution of male weight summed over 500 g intervals.

Figure 6. Frequency distribution of female pelt length summed over 4 cm intervals.

Figure 7. Frequency distribution of male pelt length summed over 5 cm intervals.

quality, body size, and fertility for the two sexes. For male and female behavior, traits were measured on different animals. Residual co-variance between traits was non-existent and set to zero, so phenotypic correlation was not calculated. Asymptotic SE of estimated (co)variance components was obtained from the average information matrix. For quantities derived from co-variance components (heritability estimates, proportions of common litter variance, and correlations), SE were obtained using a first-order Taylor series approximation (Lynch and Walsh, 1998). Variance components for behavior were estimated several times because all traits were analyzed in bivariate analyses. Variance components and SE for male and female behavior, as well as heritability, common litter variance, and associated SE, were obtained by averaging over multiple bivariate models.

Temperament was considered to differ between the sexes if additive genetic variance ± 1.96 SE for the two traits did not overlap and if genetic correlation between traits estimated for different sexes differed significantly from unity. The consequences of selection to increase confident behavior on important production traits were evaluated based on genetic correlation (± 1.96 SE) between behavioral and production traits that did not include zero. Effects of mother's age and cage mate were evaluated relative to references set to zero (effect ± 1.96 SE did not include zero). One-year-old mothers and mink living in a cage with a sibling of opposite sex were used as references.

RESULTS

Male and Female Behavior

The genetic correlation between male and female behaviors was estimated to be 0.95 (SE = 0.06; Table 2); therefore, the genetic correlation was not significantly different from 1 ($P = 0.40$). Additive genetic variance was estimated to be 0.038 (SE = 0.005) and 0.046 (SE = 0.007) for female and male behavior, respectively (Table 1). Additive genetic variance ± 1.96 SE for the two traits overlapped. Male and female behaviors were therefore considered to be the same trait in a genetic context.

Heritability

Estimated heritability was 0.19 (SE = 0.03) for both female and male behavior (Table 1). Estimated heritability of production traits ranged from 0.08 to 0.57. Values were lowest for fertility and greatest for BW and pelt length.

Common Litter Variance

Estimated common litter variance was 0.06 (SE = 0.01) and 0.05 (SE = 0.01) for females and males behavior, respectively (Table 1). For production traits, common litter variance ranged from 0.004 to 0.13, with the lowest values observed for fertility and the highest values being observed for body size traits.

Figure 8. Frequency distribution of barren/fertile females.

Figure 9. Frequency distribution of kits in first count.

Figure 10. Frequency distribution of kits in second count.

Figure 11. Frequency distribution of survival from first to second count summed over 10% intervals.

Genetic Correlations Between Behavior and Production

No genetic correlations between temperament and production traits were detected (all $P > 0.05$).

Mother's Age and Cage Mate Effects

In general, there was a tendency for both males and females from older mothers to be more exploratory than offspring from 1-yr-old mothers (Table 3). The most pronounced effects were estimated for males born to 2-yr-old mothers (effect = 0.037; SE = 0.019, $P = 0.05$) and for females born to 4-yr-old mothers (effect = 0.095; SE = 0.051, $P = 0.06$). There was no significant effect of cage mate sex or kin relationship on temperament (Table 4). However, for females, there was a trend toward increased fearfulness among mink that shared a cage with a non-kin male, but the effect was very small 0.019 (SE = 0.011, $P = 0.09$).

DISCUSSION

Similar Confidence Between Males and Females

Because the genetic correlation between male and female behavior was 0.95 (SE = 0.06), we considered male and female behavior as the same trait ($P = 0.40$). Compared with females, males exhibited a nonsignificant tendency toward more exploratory behavior, greater phenotypic variation, and a trend toward greater genetic variation, consistent with the findings of Hansen (1996) and of Malmkvist

and Hansen (2002) for mink, as well as findings for farmed silver foxes, *Vulpes vulpes* (Kenttämies et al., 2002, 2006). Birks (1981) demonstrated that, for feral mink, females are subordinate to males outside the breeding season. Furthermore, Erlinge (1977) showed that free-ranging female stoats (*Mustela erminea*) avoided males and became inactive when in the vicinity of male stoats. If a male and a female are caged together during testing, the male may prevent the female from approaching the test stimulus and thus may increase measured latency, leading to the classification of females as less exploratory. However, our results did not support this "dominance hypothesis." The fixed effect of cage mate was included in the model, and the estimated effect showed that there was no significant difference in the behavior of females, regardless of cage mate sex. Thus, females were not more subordinate to males than to other females during the time of year when tests were conducted in the home cage.

Medium Selection Potential for Confident Behavior in Farmed Mink

The estimated heritability of confident behavior was medium 0.19 (SE = 0.06), less than the estimated heritabilities for pelt quality and pelt length. Our estimates of behavior heritability were similar to the results of previous studies of farmed mink (Berg et al., 2002) and two species of farmed foxes (Kenttämies et al., 2002; 2006). This study, therefore, confirms the potential for temperament selection suggested by previous selection experiments

Table 2. Correlations between male and female behavior and between behavior and production traits estimated for males and females separately¹

Traits	r_a (SE)	r_c (SE)	r_e (SE)	r_p (SE)
Male/female	0.95 (0.06)	0.75 (0.18)	—	—
Males				
Trait/behavior	r_a (SE)	r_c (SE)	r_e (SE)	r_p (SE)
Live pelt quality	0.11 (0.07)	−0.42 (0.15)*	−0.02 (0.02)	−0.01 (0.01)
Pelt quality	0.02 (0.08)	0.002 (0.20)	0.03 (0.02)	0.02 (0.01)
Male weight	−0.01 (0.08)	0.04 (0.12)	−0.06 (0.03)	−0.03 (0.01)*
Male pelt length	0.02 (0.08)	0.03 (0.16)	−0.03 (0.03)	−0.01 (0.02)
Females				
Trait/behavior	r_a (SE)	r_c (SE)	r_e (SE)	r_p (SE)
Live pelt quality	−0.02 (0.07)	−0.04 (0.13)	0.01 (0.02)	−0.003 (0.01)
Pelt quality	0.13 (0.08)	−0.28 (0.19)	−0.01 (0.02)	0.01 (0.02)
Female weight	−0.12 (0.07)	0.06 (0.11)	0.02 (0.03)	−0.03 (0.01)*
Female pelt length	−0.04 (0.09)	0.04 (0.14)	0.01 (0.03)	−0.003 (0.02)
Barren	−0.02 (0.19)	0.999 (3.70)	0.04 (0.04)	0.05 (0.03)
First count	−0.003 (0.18)	0.19 (0.41)	0.05 (0.04)	0.05 (0.03)
Second count	0.03 (0.17)	0.36 (0.57)	0.05 (0.04)	0.06 (0.03)
Survival ²	0.09 (0.19)	0.02 (0.47)	0.02 (0.04)	0.03 (0.03)

¹ r_a is the genetic correlation, r_c is the correlation due to common litter, r_e is the environmental correlation, and r_p is the phenotypic correlation.

²Percentage of offspring that survive from first to second count.

*Significant different from zero ($P < 0.05$).

Table 3. Number of males (Nm) and females (Nf) and estimated effect for fixed class of mother age (Age)

Age, yr	Nm	Effect on males (SE)	Nf	Effect on females (SE)
1	4,555	0	4,865	0
2	1,868	0.037 (0.019)	1,845	0.025 (0.018)
3	532	0.037 (0.028)	565	0.025 (0.025)
4	139	−0.016 (0.052)	111	0.095 (0.051)

Effect of 1-yr-old mothers are given as index.

with mink (Hansen 1996; Berg et al., 2002; Hansen et al., 2010) and foxes (Belyaev, 1978; Kenttämies et al., 2002; 2006). Estimated heritability was similar for males and females, indicating similar selection potential for both sexes.

We found no significant genetic correlation between behavior and production/fertility traits, indicating that selection for more confident mink does not have a negative effect on economically important production traits. A previous study showed that live pelt quality and postmortem pelt quality (prepared for auction) were governed, to some degree, by different sets of genes, indicating that the link between live-graded and postmortem pelt quality is not as simple as one might expect (Thirstrup et al., 2016).

We found no significant genetic correlation between female weight and female behavior. Heavy females were not more fearful than smaller females ($P = 0.09$). This finding is consistent with the results reported by Hansen et al. (2010), who showed that temperament, except for stereotypic behavior, does not correlate with BW.

In this study, we found no genetic correlations of behavior with fertility, litter size, or kit survival. This result is consistent with the results of Malmkvist et al. (1997), who found that neither fertility nor litter size was affected by eight generations of selection for confident or fearful behavior. Hansen et al. (2010) also found no significant genetic correlation between temperament and litter size in farmed mink. Notably, domestication may be associated with an earlier onset of the reproduction season in mink (Malmkvist et al., 1997). The domestication process has been shown to induce the extraseasonal activation of reproductive hormones and earlier mating in other species as well (Belyaev, 1978; Naumenko and Belyaev, 1980; Trut, 1999).

Temperament May Be Weakly Affected By Mother and/or Litter Mates, But Not by Cage Mate

There was a small effect of common litter variation on phenotypic variation, with 5% of phenotypic variation being caused by common litter

Table 4. Number of males (Nm) and females (Nf) and estimated effect of fixed class of cage mate

Cage mate	Nm	Effect on males (SE)	Nf	Effect on females (SE)
Opposite sex and kin	3,244	0	3,318	0
Opposite sex and not kin	3,698	0.008 (0.012)	3,756	0.019 (0.011)
Same sex and kin	146	-0.23 (0.35)	301	-0.042 (0.036)

Effect of an animal living in a cage with a sibling of opposite sex are given as index.

variation. These findings suggest that nest environment affects postweaning exploratory/fearful behavior. This effect may reflect the common environment of a single litter. The dam of the litter and/or litter mates, as experienced at an early stage of development, may affect the temperament of an animal at a later age.

Behavioral was not significantly affected by the sex of kinship of mink's postweaning cage mates in males or females. Females living with nonkin males tended to be more fearful than females living with a litter mate of either sex ($P = 0.09$).

In nature, adult females are territorial and do not allow other mink to enter their home range when rearing a litter. Beyond the breeding season, female aggression is minimal (MacLennan and Bailey, 1969). Here, we observed very few aggressive mink (<0.5%) during standardized behavioral testing and therefore omitted the trait from subsequent analyses. The lack of any effect of cage mate kin relationship was not expected. Previous studies (Alemu et al., 2016) documented a need for including kinship as a factor in variance analyses for aggression-related traits in mink. One explanation for our findings could be that aggressive and exploratory/fearful behaviors do not share a genetic basis. Alternatively, there may be a genotype-environment interaction that should be taken into account when analyzing the genetic background of a given behavior. Of note, Alemu et al. (2016) housed mink in groups (typically two males and two females per cage) and used the number of bite marks on the leather side of pelts after killing as the index for aggressive behavior, rather than observations or direct measurements. For behavior, the effect of two kin males living together was -0.23 relative to the index: males living with a kin female. However, we only had 146 males in this group, and the SE was large 0.35 ($P = 0.50$).

Offspring from Older Mothers May Be More Confident

Offspring from older mothers tended to be more exploratory than offspring from 1-yr-old mothers. In particular, males from 2-yr-old mothers

were more exploratory than males from 1-yr-old mothers ($P = 0.05$). Females from 4-yr-old mothers were also more exploratory than females from 1-yr-old mothers ($P = 0.06$). The reason for this difference is unknown; however, we propose two possible explanations. First, in the context of mink production, reproduction improves with dam age. Dams with poor performance (due to stress, fear response, or disease) have a greater probability of being excluded from the stock (pelted) by the farmer. Consequently, fearful breeding dams are less common in subsequent generations. Because behavior is heritable, offspring from older, more exploratory females are also more exploratory. Second, older dams are more experienced and, therefore, more exploratory in general. This behavior is transmitted to the offspring as a taught behavior or via nongenetic transmission across generations (Francis et al., 1999), thus increasing exploratory behavior in offspring from older females.

CONCLUSIONS

Analyses of social effects on behavioral responses support a common genetic background for female and male behavior. Hence, confident/fearful behavior appears to be governed by the same trait in males and females. We estimated a medium heritability for temperament, which would allow breeders to select for more confident mink. We did not find any significant genetic correlation between confident/fearful behavior and any of the important fur production traits analyzed (pelt quality, pelt size, and fertility). Therefore, selection for more confident mink should not have any negative effects on important fur production traits, such as fertility or pelt quality. Consequently, we recommended that breeders select for more confident mink to increase the welfare of fur production mink as stated by Danish legislation.

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