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Genetic parameters of feeding behaviour traits in ducks bred for foie gras production

H. Chapuis [a],*, M. Lagüe [b], CMD. Bonnefont [a], I. David [a], M.-D. Bernadet [b], A. Hazard [b], H. Gilbert [a]

[a] GenPhySE, Université de Toulouse, INRAE, ENVT, 31326 Castanet Tolosan, France
[b] AVIPOLE, INRAE, 40280 Benquet, France

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A B S T R A C T

The mule duck accounts for over 90% of French foie gras production, a sector where feed represents two-thirds of production costs. This study focuses on analysing the feeding behaviours of the mule duck and its parental populations (Pekin and Muscovy) using automated feeders. To assess feed efficiency, feed conversion ratio and residual feed intake were analysed, along with six traits derived at the daily and meal levels. Genetic parameters were estimated separately in purebred populations, as well as with a joint crossbred model that estimated the parental contributions to the hybrid crossbred performances. In relation to higher feed intakes and much−reduced feeding times ($P < 0.001$), the feeding rate in the Pekin population was twice as high as in the Muscovy population (19 g/min vs 9 g/min), while the mule duck exhibited a large heterosis for this trait (29 g/min). Feeding traits exhibited moderate (0.38 ± 0.11) to high (0.65 ± 0.11) heritabilities. Similar correlation patterns were observed between feeding traits in the two parental populations. In the Pekin line, the feed conversion ratio did not significantly correlate with feeding traits except for daily feed intake. However, in the Muscovy population, it was negatively correlated with the number of meals (−0.51 ± 0.21) and positively with meal feed intake and meal duration (+0.79 ± 0.17 and + 0.71 ± 0.26, respectively). The contributions of the two parental species to the hybrid's performance differed, with the Pekin contributing more to feeding and meat traits compared to the Muscovy. They were similar only for liver weight. Additionally, unfavourable correlations between meat traits and liver traits were estimated in both pathways. Genetic relationships between feeding traits and slaughter traits varied by parental origin, suggesting different strategies for improving hybrid performance in the two parental species. However, in both pathways, genetic correlations between feed conversion ratio and meat traits (breast muscle and thigh weights) were favourable (<−0.42 ± 0.18), whereas they were unfavourable (>0.41 ± 0.20) for fatty liver weight. Altogether, improving liver traits and feed efficiency in the hybrid through selection in the parental populations could be enhanced by considering feeding traits recorded with electronic feeders, provided that adverse correlations are properly accounted for in a multitrait index.

Implications

Using automatic feeders to measure feeding behaviour traits in selection candidates can enhance the selection of parental populations (Muscovy sires and Pekin dams) for better foie gras production in their mule duck offspring. This research highlights the value of traits related to feeding time and meal frequency measured on selection candidates for improving liver traits in mule ducks. However, unfavourable correlations between feed efficiency and fatty liver traits, particularly in the sire pathway, will require the development of dedicated multitrait indexes.

Introduction

The mule duck, a sterile hybrid of female Pekin ducks (*Anas platyrhynchos*) and male Muscovy ducks (*Cairina moschata*), contributes to more than 90% of French foie gras production, one of the flagship products of French gastronomy. Selection to enhance foie gras production focuses on these parental populations. Unlike Muscovy ducks, Pekin ducks do not produce foie gras. Pekin ducks are selected based on growth, egg-laying traits, and the slaughter performance of mule half-sibs of selection candidates. The genetic correlation between mule foie gras weight and live BW in selection candidates is low for both parental populations, ranging from −0.28 (Chapuis and Larzul, 2006) to + 0.12 (Larzul, 2002) in Pekin ducks and below 0.1 in Muscovy ducks (Chapuis and Larzul, 2006).

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* Corresponding author.
E-mail address: herve.chapuis@inrae.fr (H. Chapuis).

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Therefore, effective selection for improved foie gras weight in Pekin ducks relies on accounting for the slaughter performance of related mule ducks. Similarly, Muscovy ducks are selected based on growth traits and mule half-sibs' slaughter performance.

As in most poultry productions (Waller, 2007), feeding costs represent two-thirds of total production costs in foie gras production, highlighting the importance of selecting for better feed efficiency. While feed conversion ratio (**FCR**) has been used to improve mule duck feed efficiency (Larzul et al., 2004), it negatively impacts carcass fat content and muscle adiposity (Pingel, 1999), making it less suitable for foie gras production. As demonstrated by Drouilhet et al (2014, 2016)) in a selection experiment, residual feed intake (**RFI**) (Koch et al., 1963) offers a better alternative, improving mule duck feed efficiency without compromising foie gras production.

However, accurate selection for FCR and RFI requires individual feed intake assessment, ideally in groups rather than using individual cages, to avoid welfare issues. Automatic feeders, as described by Bley and Bessei (2008), facilitate group-based feed intake measurement and behavioural analysis. Research has since shown moderate to high heritabilities for feeding behavioural traits, making them viable selection criteria, particularly in Pekin ducks for meat production (Thiele, 2016; Le Mignon et al., 2017; Zhu et al., 2019) and, to a lesser extent, in mule ducks for foie gras (Basso et al., 2014; Drouilhet et al., 2016). In addition, Chapuis et al. (2022) have described the feeding patterns of mule duck parental populations.

The genetic relationship between feeding behaviour traits in parental lines and mule duck performance remains to be fully explored. This study hypothesises a genetic basis for mule duck feeding behaviour linked to parental traits and feed efficiency, potentially exploitable through selection. The goal is to identify new selection traits in parental populations to enhance foie gras traits.

To explore the connection between feeding behaviour and production traits in the foie gras industry, three generations of mule, Pekin, and Muscovy ducks were produced. This study provides the first estimates of genetic parameters related to the feeding behaviour of foie gras ducks across these three populations (including contributions from Muscovy and Pekin to mule ducks), in relation to feed efficiency and mule duck slaughter performance. These findings aim to establish new selection criteria for parental lines to save feed without impairing fatty liver production.

Material and methods

Bird management and housing

Three successive generations of animals (Fig. 1) were bred from a dam White Pekin common duck line (n = 740), and a sire Muscovy line (n = 460). Additionally, mule half-sibs (n = 733) of these purebred ducks were also produced. Each generation comprised a single batch, except for the first two Muscovy generations, which were hatched in two batches with a 2-week lag.

The animals were reared in a 96-m^2 pen equipped with six automatic feeders (Drouilhet et al., 2016). Each feeder has an electronic scale under the access corridor that detects the presence of a duck and closes a door to prevent other animals from entering. This setup ensures that only one duck can access the feeder at a time. To facilitate duck management, the area was divided into two sections with a barrier, ensuring that each bird had effective *ad libitum* access to three feeders, thereby reducing competition among animals. During the first 7 days after hatching, the lighting was set to 24 h of light and 0 h of darkness (24L:0D). After this period, it was adjusted to 16 h of light and 8 h of darkness (16L:8D). The temperature of the building was maintained at approximately 23 °C.

Since overfed female ducks produce lower quality foie gras (more veined and smaller) compared to males, fatty liver is typically obtained by force-feeding male mule ducks, or more rarely, male Muscovy ducks. Consequently, we decided to test only male mule batches and focused on recording feeding behaviour for males in the Muscovy population, while in Pekin batches, both males and females were reared together. During the first 2 weeks, birds had free access to both the electronic feeders and an additional conventional feeder. To help the ducks adapt to the feeders, the feeder doors were kept open for the first few days after hatching. After a week, the doors would close when a duck entered the feeder. During the 2nd week for Pekin ducks and the 3rd week for Muscovy and mule ducks, birds were electronically tagged at the base of the neck with a transponder. Animals were thus identified using a radio frequency antenna system when they entered and exited a feeding station. Conventional feeders were removed 1 day before the start of the trial.

Feeding traits were assessed over a 5-week period, ranging from day 15 to day 49 for the Pekin population and from day 22 to day 56 for Muscovy and mule ducks. The gregarious behaviour of Muscovy ducks resulted in a high number of simultaneous visits to the same feeder at a young age, making accurate feed consumption recording challenging before 3 weeks of age (Cobo et al., 2022). Consequently, the recording period for Muscovy ducks was delayed compared to Pekin ducks. Up to the end of the recording period (day 56), mule ducks were reared on the same schedule as Muscovy ducks (Fig. 2).

The three genetic types were fed the same diet until the end of their recording period, albeit with different feeding schedules. Initially, they were provided with a starter diet from hatching until day 14 (for Pekin) and day 21 (for Muscovy and mule ducks). Subsequently, during the recording period (from day 15 to day 49 for Pekin and from day 22 to day 56 for Muscovy and mule ducks), the birds had *ad libitum* access, via automatic feeders, to a 4-mm pelleted diet with apparent metabolisable energy nitrogen-corrected of 11.9 MJ/kg and digestible CP of 155 g/kg.

After the recording period, from day 64 to day 83, only mule ducks were prepared for the force-feeding phase. During this preparation period, they had limited access to the same feed (1 h per day). Starting from day 84, the ducks were subjected to overfeeding for 11 days with 23 meals (evening meal only on the first day and then two meals a day) consisting of Palma 146 mash from Maïsadour (98% Maize and 2% Premix, DM = 53%, Apparent metabolisable energy nitrogen-corrected = 13.6 MJ/kg with digestible CP = 72 g/kg). The amount of feed administered during force-feeding was gradually increased and adjusted based on the animals' BW.

At the conclusion of the test period, an individual Total body electrical conductivity (**TOBEC**) score was recorded using equipment from EM-SCAN Inc., Springfield, IL, USA, to estimate the lipid mass in the animals' bodies. This measure was carried out for all batches of Pekin and Muscovy ducks, but it was unavailable for one of the three mule batches.

Data acquisition

Feeding behavioural traits

Each time an animal was identified entering a feeder, it triggered the recording of a new visit. Records included the bird's identification, start and end date and time, feed intake, and BW. Average feeding behaviour traits were then calculated over the 5-week period. The definitions of average daily feed intake (**ADFI**) and average daily feeding time (**ADFT**) are straightforward. Average feeding rate (**AFR**) was computed as the ratio of feed intake

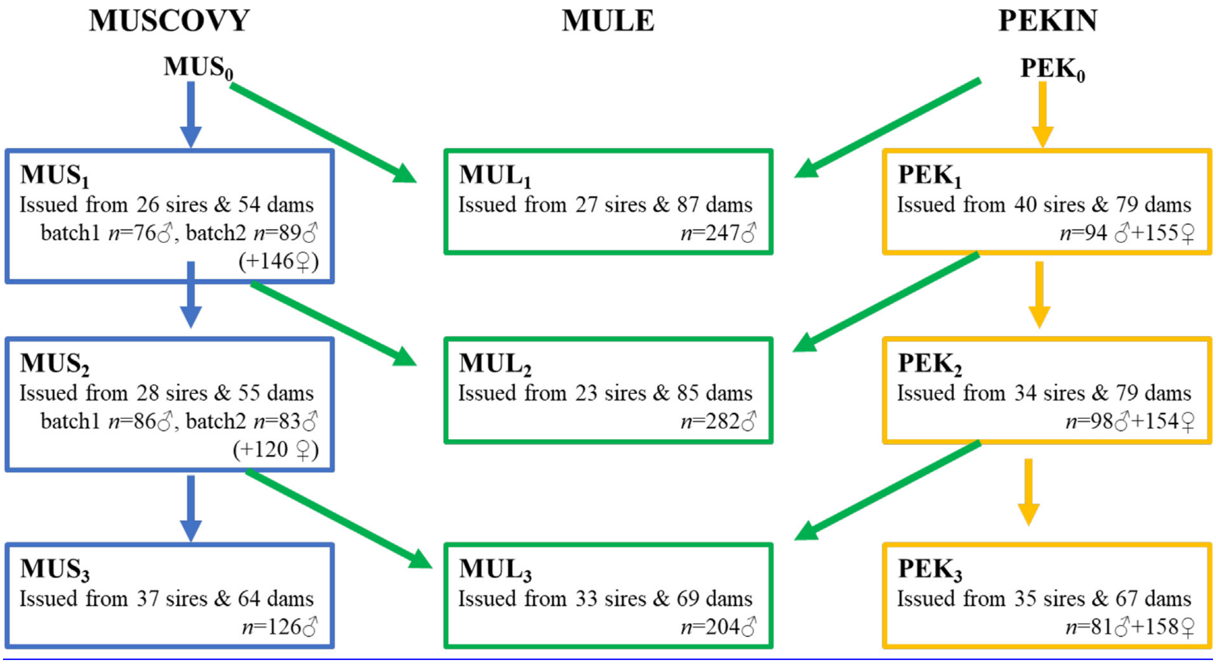

Fig. 1. Organisation of the pedigreed experimental duck cohorts.

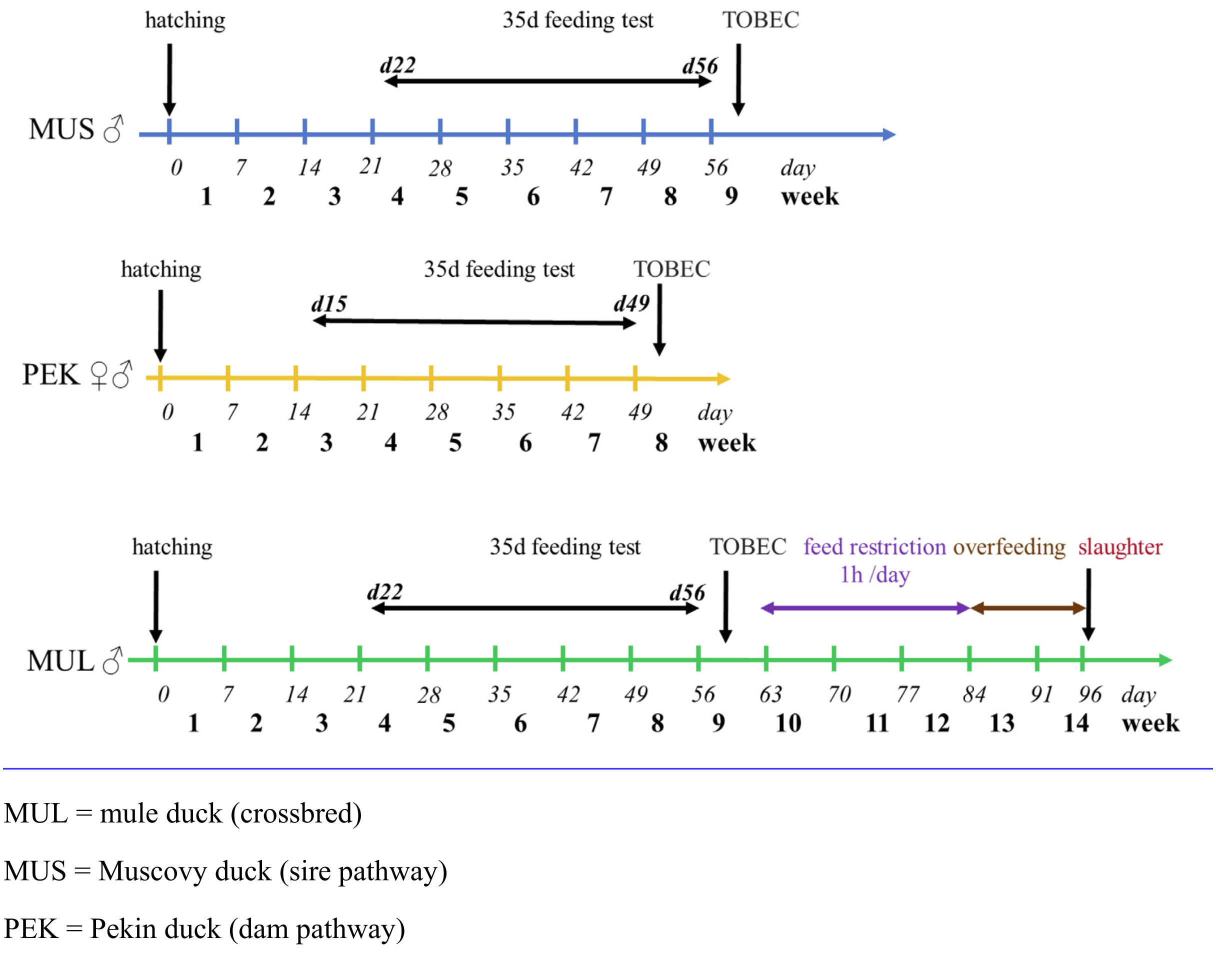

Fig. 2. Experimental design for foie gras ducks.

over feeding time for each visit and averaged over the whole period. Visits were aggregated into meals to allow for reliable comparisons of feeding behaviours between populations and flocks.

Using, the Mixtools R package (Benaglia et al., 2009), a mixture of two log-normal distributions was applied to the time intervals between successive visits of the same animal to the feeder for each batch This method helped determine the meal criterion, defined as the point where the two distributions intersect (Howie et al., 2009) (see Supplementary Figure S1 for an example). For each duck, visits were considered part of a single meal if the time interval between visits was shorter than the meal criterion. As a result, the average number of meals per day (**ANM**), average meal duration (**AMD**), and average food consumption per meal (**AMFI**) were also recorded.

Slaughter traits

After force-feeding, the mule ducks were subjected to electronarcosis and slaughtered. Twenty minutes *postmortem* their liver was eviscerated and weighed to determine liver weight. After cooling the carcass in a room at 4 °C for 24 h, the right thigh, including the bone, muscle and skin, was collected and weighed to determine thigh weight. At the same time, the breast muscle, also known as *"magret"* (*pectoralis major*), was removed from the carcass and the muscle was carefully separated from the skin and weighed to determine the skinned breast muscle weight. The technological properties of the liver were assessed using a cooking test to measure the liver melting rate, which is the percentage of fat release after pasteurisation of 60 g of liver for 60 min at 85 °C.

Efficiency traits

Feed efficiency during the 5-week recording period was evaluated by calculating the feed conversion ratio, which is the ratio of total feed intake to total weight gain. Additionally, two variations of residual feed intake (RFI_1 and RFI_2) were computed. These are the differences between an animal's actual feed intake and the expected feed intake based on its production and maintenance needs. A high RFI value indicates poor feed efficiency, meaning the animal consumes more than expected.

The RFI values are the residuals of a multiple linear regression of DFI on the average metabolic BW to account for maintenance requirements and on average daily gain (**ADG**) in order to account for production requirements (RFI_1). The TOBEC score was introduced as an extra factor in RFI_2 to account for the animal's body adiposity. The average metabolic BW was computed as $\bar{BW}^{0.75}$ where $\bar{BW}$ is the average BW measured over the 5-week period. The ADG was computed by differentiating BWs at the start and end of the recording period divided by the period length.

For each individual i, RFIs were derived as follows: $DFI_i = \mu + \gamma_{batch} + \alpha_1 \times \bar{BW}_i^{0.75} + \beta_1 \times ADG_i + RFI_{1i}$ and $DFI_i = \mu + \gamma_{batch} + \alpha_2 \times \bar{BW}_i^{0.75} + \beta_2 \times ADG_i + \delta_2 \times TOBEC_i + RFI_{2i}$

As we could not perform the TOBEC measurement in all three mule batches, RFI_2 was not computed for the mule population.

Statistical analysis

To normalise the data and improve the symmetry of the distributions, the ADFT and AMD were log-transformed before analysis. An illustration of the effect of the log transformation on the distribution of time-related feeding traits is provided in Supplementary Figure S2. Values exceeding three SDs from the mean within a line were considered as outliers and removed from the analyses. They represented less than 0.5% of raw data in the mule population, 0.8% in Pekin and 1.3% in Muscovy. Phenotypic comparisons of performance between lines were obtained using a linear model taking into account the effects of line (three levels: Pekin, Muscovy and mule) and sex (two levels) in the Pekin line only, using the R emmeans package (Lenth, 2022).

Genetic parameters were estimated using the REML method (Harville, 1977) with ASReml software (Gilmour et al., 2015) and models tailored to the population under consideration:

Purebred analyses

An animal linear mixed model was considered for each trait as:

$$y_{ijk} = \mu + \beta_j + \gamma_k + u_i + \varepsilon_{ijk} \qquad (1)$$

where y_{ijk} is the phenotype of animal i of sex k born in batch j, μ is the general mean, β_j and γ_k are the fixed effects of batch and sex (for the Pekin line only), respectively, u_i is the additive genetic effect, and ε_{ijk} is the residual. Both the genetic and the residual effects are normally distributed. Residuals are considered independent, whereas additive effects are structured according to the pedigree relationship matrix A. First, univariate analyses were run to compute heritabilities, and then, multivariate models were applied with the same effects to obtain correlations between traits.

Mule trait analyses

Mule traits were analysed using a parental model:

$$y_{jkml} = \mu + \beta_k + s_m + d_l + \varepsilon_{jkml} \qquad (2)$$

where y_{jkml} is the phenotype of the jth animal born in batch k from sire m and dam l. μ and β_k stand for the same variables as previously stated. s_m and d_l represent the random genetic contributions of the Muscovy sire and the Pekin dam, respectively, to the performance of their mule offspring.

Two different numerator relationship matrices, say A_{MUS} and A_{PEK}, were built to fit the model, and the random effects had the following variances:

$$Var\begin{pmatrix} s \\ d \\ \varepsilon \end{pmatrix} = \begin{pmatrix} \sigma_s^2 A_{MUS} & 0 & 0 \\ 0 & \sigma_d^2 A_{PEK} & 0 \\ 0 & 0 & \sigma_\varepsilon^2 I \end{pmatrix}$$

For each mule trait, the parental contribution ratios were defined as follows:

- sire Muscovy contribution ratio $c_s^2 = \frac{\sigma_s^2}{\sigma_s^2 + \sigma_d^2 + \sigma_\varepsilon^2}$
- dam Pekin contribution ratio $c_d^2 = \frac{\sigma_d^2}{\sigma_s^2 + \sigma_d^2 + \sigma_\varepsilon^2}$

This model was then extended in order to estimate genetic correlations between traits measured in the mule population and traits measured in one parental population: Models 3 and 4 were used to simultaneously estimate the genetic correlations between the mule and Muscovy populations or the Pekin and mule populations, respectively, for different traits (two traits at a time):

$$\begin{cases} y_{MUL} = X_{MUL}\beta_{MUL} + Z_{MUL}s + W_{MUL}d + \varepsilon_{MUL} \\ y_{MUS} = X_{MUS}\beta_{MUS} + Z_{MUS}u_{MUS} + \varepsilon_{MUS} \end{cases} \qquad (3)$$

with

$$Var\begin{pmatrix} s \\ u_{MUS} \\ d \\ \varepsilon_{MUL} \\ \varepsilon_{MUS} \end{pmatrix} = \begin{pmatrix} \begin{pmatrix} \sigma_s^2 & \rho_s\sigma_s\sigma_{MUS} \\ \rho_s\sigma_s\sigma_{MUS} & \sigma_{MUS}^2 \end{pmatrix} \otimes A_{MUS} & 0 & 0 \\ 0 & \sigma_d^2 A_{PEK} & 0 \\ 0 & 0 & \begin{matrix} \sigma_{\varepsilon_{MUL}}^2 I & 0 \\ 0 & \sigma_{\varepsilon_{MUS}}^2 I \end{matrix} \end{pmatrix}$$

and

$$\begin{cases} y_{MUL} = X_{MUL}\beta_{MUL} + Z_{MUL}s + W_{MUL}d + \varepsilon_{MUL} \\ y_{PEK} = X_{PEK}\beta_{PEK} + Z_{PEK}u_{PEK} + \varepsilon_{PEK} \end{cases} \qquad (4)$$

with

$$Var\begin{pmatrix} d \\ u_{PEK} \\ s \\ \varepsilon_{MUL} \\ \varepsilon_{PEK} \end{pmatrix} = \begin{pmatrix} \begin{pmatrix} \sigma_d^2 & \rho_d\sigma_d\sigma_{PEK} \\ \rho_d\sigma_d\sigma_{PEK} & \sigma_{PEK}^2 \end{pmatrix} \otimes \mathrm{A}_{\mathrm{PEK}} & 0 & 0 \\ 0 & \sigma_s^2\mathrm{A}_{\mathrm{MUS}} & 0 \\ 0 & 0 & \begin{matrix} \sigma_{\varepsilon_{MUL}}^2\mathrm{I} & 0 \\ 0 & \sigma_{\varepsilon_{PEK}}^2\mathrm{I} \end{matrix} \end{pmatrix}$$

where y_x are the vectors of performances measured in population x, X_x, Z_x, and W_x are known incidence matrices, β_x represents the vectors of fixed effects for population x (batch effect for all populations, slaughter date for mule slaughter traits and sex effect for Pekin only), while s and d are the vectors of genetic parental contributions to the mule performances. u_{MUS} and u_{PEK} are the vectors of additive genetic effects in the Muscovy and Pekin populations, respectively. ρ_s is the genetic correlation between a trait measured in the mule population and another trait measured in the Muscovy population, while the genetic correlation between a trait measured in the mule population and another trait measured in the Pekin population is ρ_d.

Results

Comparison of performances between populations

The mean values of each trait are reported for each population in Table 1. Except for FCR, the average values of all traits were significantly different in the three populations at the threshold P-value of 0.05.

Pekin vs Muscovy performances

Pekin ducks spent nearly half as much time feeding each day as Muscovy ducks but consumed 9% more feed, resulting in a feeding rate more than twice as high for Pekin ducks. The average number of meals per day was smaller in Muscovy (3.57 vs 4.46, $P < 0.001$), and the meals were roughly 2.4 times longer than in the Pekin line (460 vs 190 s, $P < 0.001$). Muscovy ducks exhibited the lowest values for ADFI, AFR, ANM and FCR, and the highest values for ADFT, AMD and ADG. The only trait where Muscovy ducks had an intermediate value compared to the other lines was AMFI. Pekin ducks had the lowest AMFI and intermediate values for ADFI, ADFT, AFR, and AMD, while mule ducks ranked second for ANM and ADG.

Crossbred vs purebred performances

The mule performances approximately averaged the parental values for ANM and ADG. For FCR, AMD, and ADFT, mule performances were closer to those of Pekin than to Muscovy. Regarding ADFI and AMFI, mule ducks exhibited moderate positive heterosis over their parents. The heterosis was even more pronounced for AFR, which in the mule population was over three times greater than the Muscovy value and 1.5 times greater than the Pekin value. For FCR, mule and Pekin ducks did not differ significantly, but both were significantly higher than Muscovy ducks.

Genetic parameters for feeding traits in the parental lines

Genetic parameters for feeding behaviour traits in the sire and dam parental lines are displayed in Table 2. In both lines, feeding behaviour traits were highly heritable, with estimates ranging from 0.46 to 0.62 in the Pekin line and from 0.35 to 0.65 in the Muscovy line, depending on the trait. Except for AFR and AMD, which tended to be more heritable in the Pekin population ($P < 0.10$), estimated heritabilities did not differ between the two populations ($P > 0.10$).

For most traits, genetic correlations showed similar patterns in both populations: ADFI was positively correlated with AMFI and, in addition, slightly negatively correlated with ANM. ADFT was positively correlated with ANM and AMD, strongly negatively correlated with AFR, and moderately negatively correlated with AMFI only in Pekin. In both Muscovy and Pekin populations, AFR was negatively correlated with ANM and AMD, and positively linked with AMFI. ANM and AMFI exhibited a strong negative correlation, while the negative link between ANM and AMD was significantly different from zero only in Pekin. Additionally, a moderate positive correlation was found between AMFI and AMD.

Genetic relationships between feed efficiency traits, average daily gain and feeding behaviour traits in the parental lines

Table 3 presents the genetic parameters for efficiency traits and average daily gain in the two parental populations. The heritability estimates for feed efficiency traits were moderate in the Muscovy line, ranging from 0.22 ± 0.10 to 0.24 ± 0.10, and higher in the Pekin line, ranging from 0.33 ± 0.07 to 0.48 ± 0.08. For ADG, heritability estimates were moderate to high, at 0.37 ± 0.11 in the Muscovy line and 0.53 ± 0.07 in the Pekin line. Feed efficiency traits exhibited high correlations in both populations ($\varrho > 0.71 \pm 0.12$). There were no significant correlations between ADG and feed efficiency traits, except for a notable correlation with feed conversion ratio in the Pekin line ($\varrho = -0.34 \pm 0.12$).

Table 4 displays the genetic correlations between feeding behavioural traits, feed efficiency traits and ADG in each parental line. ADG was positively correlated with ADFI and AMFI in both lines, and with AMD in the Pekin line. Feed efficiency traits were positively correlated with ADFI. In the Muscovy line, FCR was also significantly correlated with ANM ($\varrho = -0.51 \pm 0.21$), AMFI ($\varrho = 0.79 \pm 0.17$) and AMD ($\varrho = 0.71 \pm 0.26$). In the Pekin line, RFIs were positively correlated with AMFI and negatively correlated with ANM. Additionally, in this line, RFI_2 exhibited a moderate positive genetic correlation with AFR.

Table 1
Mean values (Least square means[1] ± SE) of feeding behaviour traits in the three duck populations.

Trait	MUSCOVY	MULE	PEKIN
Average Daily Feed Intake (g)	204 ± 1.54^A	236 ± 1.38^B	224 ± 0.96^C
Average Daily Feeding Time (s)	1 603 ± 17.7^C	576 ± 16.0^A	810 ± 11.1^B
Average Feeding Rate (g/min)	9.05 ± 0.292^A	29.44 ± 0.265^C	18.88 ± 0.184^B
Average Number of Meals	3.57 ± 0.066^A	4.01 ± 0.060^B	4.46 ± 0.042^C
Average Meal Feed Intake (g)	58.9 ± 1.04^B	64.3 ± 0.94^C	53.1 ± 0.65^A
Average Meal Duration (s)	460 ± 6.2^C	152 ± 5.7^A	190 ± 3.9^B
Average Daily Gain (g/d)	80.9 ± 0.45^C	73.7 ± 0.41^B	69.0 ± 0.28^A
Feed Conversion Ratio (g/g)	2.57 ± 0.013^A	3.23 ± 0.012^B	3.25 ± 0.008^B

[1] Least square means from a linear model including the fixed effect of line, batch and sex (PEKIN population only). Within a row, different letter superscripts indicate a significant difference between populations ($P < 0.05$).

Table 2
Genetic parameters (heritability estimates in bold on the diagonal, genetic correlations above the diagonal, with their SEs) for feeding behaviour traits in the parental lines of the mule duck (Muscovy sire line and Pekin dam line). Values in bold denote a parameter of absolute value greater than or equal to 1.96 times the SE, meaning that they differ from nullity with a 95% confidence level. When absolute values lie between 1.64 (90% confidence) and 1.96 times the SE, they are in italics.

Population	Trait	ADFI	ADFT	AFR	ANM	AMFI	AMD
MUSCOVY	ADFI	**0.50 ± 0.12**	0.21 ± 0.20	0.16 ± 0.20	*−0.28 ± 0.18*	**0.66 ± 0.11**	0.37 ± 0.22
	ADFT		**0.53 ± 0.12**	**−0.88 ± 0.05**	**0.36 ± 0.17**	−0.19 ± 0.17	**0.75 ± 0.09**
	AFR			**0.38 ± 0.11**	**−0.42 ± 0.19**	**0.44 ± 0.17**	**−0.61 ± 0.14**
	ANM				**0.56 ± 0.11**	**−0.91 ± 0.04**	−0.30 ± 0.19
	AMFI					**0.65 ± 0.11**	*0.36 ± 0.18*
	AMD						**0.35 ± 0.11**
PEKIN	ADFI	**0.49 ± 0.08**	0.11 ± 0.13	0.16 ± 0.12	−0.16 ± 0.13	**0.40 ± 0.11**	0.23 ± 0.14
	ADFT		**0.55 ± 0.07**	**−0.95 ± 0.02**	**0.43 ± 0.10**	**−0.41 ± 0.10**	**0.60 ± 0.08**
	AFR			**0.59 ± 0.07**	**−0.42 ± 0.10**	**0.49 ± 0.09**	**−0.54 ± 0.09**
	ANM				**0.56 ± 0.07**	**−0.95 ± 0.08**	**−0.45 ± 0.10**
	AMFI					**0.62 ± 0.07**	**0.45 ± 0.10**
	AMD						**0.46 ± 0.07**

ADFI = Average Daily Feed Intake; ADFT = Average Daily Feeding Time; AFR = Average Feeding Rate; ANM = Average Number of daily Meals; AMFI = Average Meal Feed Intake; AMD = Average Meal Duration.

Table 3
Genetic parameters (heritability estimates on the diagonal, genetic correlations above the diagonal, with their SEs) for feed efficiency traits in the parental lines of the mule duck (Muscovy sire line and Pekin dam line). Values in bold denote a parameter of absolute value greater than or equal to 1.96 times the SE, meaning that they differ from nullity with a 95% confidence level.

Population	Trait	ADG	FCR	RFI1	RFI2
MUSCOVY	ADG	**0.37 ± 0.11**	0.31 ± 0.28	0.34 ± 0.26	0.12 ± 0.29
	FCR		**0.22 ± 0.10**	**0.80 ± 0.12**	**0.71 ± 0.12**
	RFI1			**0.22 ± 0.10**	**0.97 ± 0.02**
	RFI2				**0.24 ± 0.10**
PEKIN	ADG	**0.53 ± 0.07**	**−0.34 ± 0.12**	0.15 ± 0.13	0.17 ± 0.14
	FCR		**0.48 ± 0.08**	**0.82 ± 0.05**	**0.76 ± 0.06**
	RFI1			**0.49 ± 0.08**	**0.91 ± 0.01**
	RFI2				**0.33 ± 0.07**

ADG = Average Daily Gain; FCR = Feed Conversion Ratio; RFI_1 and RFI_2 are two derivations of Residual Feed Intake accounting (RFI_1) or not (RFI_2) for the body fat content estimated through Total Body Electrical Conductivity (TOBEC).

Table 4
Genetic correlations of average daily weight gain and feed efficiency traits with feeding behaviour traits in the parental lines of the mule duck (Muscovy sire line and Pekin dam line). Values in bold denote a correlation of absolute value greater than or equal to 1.96 times the SE, meaning that they differ from nullity with a 95% confidence level. When absolute values lie between 1.64 (90% confidence) and 1.96 times the SE, they are in italics.

Population	Trait	ADFI	ADFT	AFR	ANM	AMFI	AMD
MUSCOVY	ADG	**0.93 ± 0.04**	0.07 ± 0.22	0.21 ± 0.22	−0.18 ± 0.20	**0.52 ± 0.15**	0.00 ± 0.25
	FCR	**0.69 ± 0.17**	0.33 ± 0.29	0.00 ± 0.27	**−0.51 ± 0.21**	**0.79 ± 0.17**	**0.71 ± 0.26**
	RFI_1	**0.63 ± 0.19**	*0.43 ± 0.25*	−0.16 ± 0.28	−0.11 ± 0.25	*0.36 ± 0.22*	0.39 ± 0.29
	RFI_2	*0.42 ± 0.23*	0.33 ± 0.25	−0.15 ± 0.28	−0.09 ± 0.25	0.28 ± 0.22	0.39 ± 0.29
PEKIN	ADG	**0.76 ± 0.06**	0.16 ± 0.12	0.07 ± 0.11	−0.11 ± 0.12	**0.33 ± 0.11**	**0.27 ± 0.12**
	FCR	**0.35 ± 0.12**	−0.10 ± 0.13	0.13 ± 0.12	−0.11 ± 0.14	0.14 ± 0.13	−0.05 ± 0.14
	RFI_1	**0.70 ± 0.07**	−0.13 ± 0.13	0.28 ± 0.23	**−0.27 ± 0.13**	**0.44 ± 0.11**	0.09 ± 0.14
	RFI_2	**0.71 ± 0.09**	−0.12 ± 0.15	**0.29 ± 0.14**	**−0.29 ± 0.15**	**0.47 ± 0.13**	0.12 ± 0.16

ADFI = Average Daily Feed Intake; ADFT = Average Daily Feeding Time; AFR = Average Feeding Rate; ANM = Average Number of daily Meals; AMFI = Average Meal Feed Intake; AMD = Average Meal Duration; ADG = Average Daily Gain; FCR = Feed Conversion Ratio; RFI_1 and RFI_2 are two derivations of Residual Feed Intake accounting (RFI_1) or not (RFI_2) for the body fat content estimated through Total Body Electrical Conductivity (TOBEC).

Parental contributions for feeding traits and correlations with purebred traits

Table 5 presents the respective contributions computed on the sire and dam pathways for feeding behavioural traits, ADG, and feed efficiency traits observed in the mule populations, as well as their correlations with purebred traits. For all traits, the Pekin contribution ratios were higher than those for Muscovy, ranging from 0.10 ± 0.04 to 0.44 ± 0.05 in Pekin, compared to a maximum of 0.10 ± 0.04 for Muscovy. Although the sire contribution ratios were low, they significantly differed from zero for behavioural and efficiency traits. AFR was the only trait showing a significant and positive correlation between the Muscovy and mule populations. Conversely, on the dam path, all behavioural traits were positively correlated between purebred Pekin and mule populations. The estimated ratios in this pathway were significantly different from zero, with higher values for feed intake traits (ADFI and AMFI; $c_d^2 > 0.40 \pm 0.05$) than for duration traits ($c_d^2 = 0.10 \pm 0.04$ for ADFT and $c_d^2 = 0.21 \pm 0.05$ for AMD), and they were intermediate for AFR and ANM. For behavioural traits, correlations were higher for traits

Table 5

Parental contribution to feeding traits and genetic correlations with purebred traits in the parental lines of the mule duck (Muscovy sire line and Pekin dam line). Values in bold denote a genetic correlation or a parental contribution ratio of absolute value greater than or equal to 1.96 times the SE, meaning that they differ from nullity with a 95% confidence level. When absolute values lie between 1.64 (90% confidence) and 1.96 times the SE, they are in italics.

Trait	Sire Muscovy line		Dam Pekin line	
	c_s^2	$\rho_{MUS,MUL}$	c_d^2	$\rho_{PEK,MUL}$
ADFI	**0.08 ± 0.04**	0.46 ± 0.30	**0.44 ± 0.05**	**0.80 ± 0.09**
ADFT	**0.10 ± 0.04**	0.26 ± 0.28	**0.10 ± 0.04**	**0.94 ± 0.20**
AFR	**0.09 ± 0.04**	*0.54 ± 0.30*	**0.29 ± 0.05**	**0.75 ± 0.10**
ANM	**0.08 ± 0.04**	−0.05 ± 0.31	**0.35 ± 0.05**	**0.46 ± 0.13**
AMFI	*0.05 ± 0.03*	0.07 ± 0.33	**0.40 ± 0.05**	**0.51 ± 0.12**
AMD	**0.10 ± 0.04**	0.38 ± 0.29	**0.21 ± 0.05**	**0.47 ± 0.17**
ADG	0.05 ± 0.03	**0.87 ± 0.36**	**0.36 ± 0.05**	**0.82 ± 0.09**
FCR	**0.09 ± 0.04**	0.50 ± 0.35	**0.19 ± 0.05**	**0.44 ± 0.17**
RFI_1	**0.07 ± 0.03**	**0.70 ± 0.31**	**0.13 ± 0.05**	*0.40 ± 0.21*

ADFI = Average Daily Feed Intake; ADFT = Average Daily Feeding Time; AFR = Average Feeding Rate; ANM = Average Number of daily meals; AMFI = Average Meal Feed Intake; AMD = Average Meal Duration; ADG = Average Daily Gain, FCR = Feed Conversion Ratio; RFI_1 = Residual Feed Intake (not accounting for the body adiposity).
c_s^2 = sire Muscovy contribution ratio to the mule performance; $\rho_{MUS,MUL}$ = genetic correlation between purebred and crossbred performance in the sire (Muscovy) pathway; c_d^2= dam Pekin contribution ratio to the mule performance; $\rho_{PEK,MUL}$ = genetic correlation between purebred and crossbred performance in the dam (Pekin) pathway.

when computed on a daily scale than on the meal scale ($\varrho = 0.80 \pm 0.09$ vs $\varrho = 0.51 \pm 0.12$ for feed quantity and $\varrho = 0.94 \pm 0.20$ vs $\varrho = 0.47 \pm 0.17$ for feeding time).

The genetic correlation between purebred and crossbred ADG was highly positive (above 0.8) and significant in both parental populations. The positive correlation between purebred and crossbred efficiency traits was significantly different from zero, except for FCR in the sire pathway.

Genetic parameters of mule slaughter traits

The elementary statistics for the four slaughter performances of primary importance for the fatty liver market – liver weight, skinned *magret* weight and thigh weight recorded in mule ducks, plus liver melting rate – are given in Table 6. Liver weights met the standards for foie gras production, validating the overfeeding management.

Parental contributions for meat traits (skinned breast muscle and thigh weights) were higher in the dam pathway (0.26 ± 0.08 and 0.20 ± 0.05) than in the sire pathway (0.13 ± 0.05 and 0.06 ± 0.05, respectively). For liver weight, contributions were similar in both parental populations (0.17 ± 0.05 vs 0.15 ± 0.05). Negative genetic correlations between liver weight and meat traits were observed in both pathways, with a more pronounced trend in the sire pathway, while meat traits were positively correlated with each other. The liver meting rate also tended to exhibit a higher dam contribution than the sire contribution (0.20 ± 0.06 vs 0.13 ± 0.05). It was highly correlated with liver weight in both pathways and was strongly and negatively correlated with thigh weight in the sire pathway alone.

Correlations between purebred feeding traits and mule slaughter performances

Genetic correlations with feeding and efficiency traits were estimated for these slaughter traits and are presented in Table 7.

For liver and skinned *magret* weights, a set of feeding traits in at least one of the purebred parents could be found with a correlation significantly different from nullity ($P < 0.05$). For thigh weight, significant correlations were observed only in the dam pathway, specifically with traits related to feed intake at the meal or daily level. In the Muscovy population, both ANM and AMFI were positively correlated with liver melting rate. Additionally, in this population, liver melting rate was positively correlated with ADG, FCR and RFI_2. Conversely, in the Pekin population, liver melting rate was only correlated with FCR.

FCR was the only trait that had significant correlations in both parental pathways for all slaughter traits. It was positively correlated with liver weight and negatively correlated with skinned breast muscle and thigh weights, indicating that selecting for decreased FCR would negatively impact liver weight but not the two muscle weights. In the Pekin population, none of the RFIs was significantly correlated with any slaughter trait. Conversely, in the Muscovy population, both RFIs significantly exhibited a non-zero correlation with liver and skinned *magret* weights, while only RFI_2 was correlated with thigh weight.

Table 6

Elementary statistics and genetic parameters for slaughter mule performances depending on the parental population (Pekin or Muscovy duck). Parental contributions are on the diagonal and genetic correlations above the diagonal, with their SEs. Values in bold denote a parameter of absolute value greater than or equal to 1.96 times the SE, meaning that they differ from nullity with a 95% confidence level.

Item	Trait	Liver traits		Meat traits	
		LW	LMR	SBMW	TW
Descriptive statistics	Mean ± SD	552 ± 123.1 (g)	26.1 ± 0.14 (%)	303 ± 27.7(g)	482 ± 44.9 (g)
MUSCOVY (sire pathway)	LW	**0.15 ± 0.05**	**0.82 ± 0.11**	−0.42 ± 0.27	**−0.83 ± 0.35**
	LMR		**0.13 ± 0.05**	−0.15 ± 0.30	**−0.89 ± 0.37**
	SBMW			**0.13 ± 0.05**	**0.62 ± 0.27**
	TW				0.06 ± 0.05
PEKIN (dam pathway)	LW	**0.17 ± 0.05**	**0.76 ± 0.11**	−0.04 ± 0.20	−0.25 ± 0.21
	LMR		**0.20 ± 0.06**	0.00 ± 0.19	−0.09 ± 0.21
	SBMW			**0.26 ± 0.08**	**0.53 ± 0.14**
	TW				**0.20 ± 0.05**

LW = fatty liver weight; LMR = liver melting rate; SBMW = skinned breast muscle weight; TW = thigh weight.

Table 7

Genetic correlations between purebred feeding and efficiency traits and mule slaughter performances in the parental lines of the mule duck (Muscovy sire line and Pekin dam line). Values in bold denote a correlation of absolute value greater than or equal to 1.96 times the SE, meaning that they differ from nullity with a 95% confidence level. When absolute values lie between 1.64 (90% confidence) and 1.96 times the SE, they are in italics.

	Liver traits				Meat traits			
	Liver Weight		Liver Melting Rate		Thigh Weight		Skinned Breast Muscle Weight	
Item	MUSCOVY	PEKIN	MUSCOVY	PEKIN	MUSCOVY	PEKIN	MUSCOVY	PEKIN
ADFI	0.10 ± 0.28	0.12 ± 0.22	–0.17 ± 0.29	0.27 ± 0.21	0.26 ± 0.34	**0.66 ± 0.16**	0.23 ± 0.28	**0.37 ± 0.16**
ADFT	0.35 ± 0.24	**0.43 ± 0.19**	0.06 ± 0.26	0.29 ± 0.19	–0.19 ± 0.32	–0.15 ± 0.19	–**0.62 ± 0.23**	*–0.30 ± 0.16*
AFR	–0.01 ± 0.28	–**0.40 ± 0.19**	0.27 ± 0.30	–0.23 ± 0.19	–0.24 ± 0.39	0.14 ± 0.18	*0.47 ± 0.27*	**0.32 ± 0.16**
ANM	*–0.44 ± 0.23*	0.03 ± 0.19	–**0.66 ± 0.21**	0.03 ± 0.19	0.46 ± 0.32	–0.28 ± 0.18	0.34 ± 0.26	–0.25 ± 0.16
AMFI	0.31 ± 0.22	–0.06 ± 0.20	*0.42 ± 0.24*	0.00 ± 0.19	–0.28 ± 0.32	**0.43 ± 0.17**	–0.19 ± 0.25	**0.32 ± 0.15**
AMD	**0.52 ± 0.25**	*0.36 ± 0.20*	0.36 ± 0.28	0.23 ± 0.19	–0.47 ± 0.33	0.14 ± 0.19	–**0.85 ± 0.19**	–0.06 ± 0.17
ADG	–0.21 ± 0.29	–0.14 ± 0.21	*–0.54 ± 0.29*	–0.01 ± 0.19	**0.67 ± 0.30**	**0.84 ± 0.12**	**0.58 ± 0.24**	**0.66 ± 0.13**
FCR	**0.63 ± 0.28**	**0.41 ± 0.20**	**0.69 ± 0.31**	**0.39 ± 0.19**	–**0.86 ± 0.36**	–**0.42 ± 0.18**	–**0.75 ± 0.27**	–**0.44 ± 0.16**
RFI_1	*0.52 ± 0.30*	0.15 ± 0.21	0.49 ± 0.34	0.21 ± 0.21	–0.50 ± 0.41	–0.09 ± 0.19	–**0.77 ± 0.30**	–0.10 ± 0.19
RFI_2	**0.60 ± 0.28**	0.20 ± 0.25	**0.70 ± 0.31**	0.29 ± 0.24	*–0.63 ± 0.38*	–0.12 ± 0.22	–**0.69 ± 0.29**	–0.04 ± 0.21

ADFI = Average Daily Feed Intake; ADFT = Average Daily Feeding Time; AFR = Average Feeding Rate; ANM = Average Number of daily meals; AMFI = Average Meal Feed Intake; AMD = Average Meal Duration; ADG = Average Daily Gain; FCR = Feed Conversion Ratio; RFI_1 and RFI_2 are two derivations of Residual Feed Intake accounting (RFI_1) or not (RFI_2) for the body fat content estimated through Total Body Electrical Conductivity (TOBEC).

Discussion

This is the first genetic study to investigate genetic parameters of feeding traits in the three duck populations and their relationships with traits for foie gras production.

Computation of feeding traits

The logarithm values of the meal criterion differed only slightly between populations and between batches within populations: 7.33 ± 0.07 for mule, 7.62 ± 0.05 for Muscovy and 7.72 ± 0.10 for Pekin. There was no significant difference in the meal criterion between the Muscovy and Pekin populations, with a slightly lower value observed in the crossbred population. After confirming that these differences did not affect meal characteristics, a specific meal criterion was calculated for each batch rather than using a common value for all batches within a population.

For the Pekin line, the meal criterion (i.e., the interval between meals) was approximately 1725 s (natural log of 7.45), consistent with the value reported by Howie et al. (2010) in another Pekin population. In contrast, Zhu et al. (2017) reported a shorter interval (natural log of 7.03).

Computation of efficiency traits

Two methods for computing residual feed intake were compared, considering that an accurate derivation of RFI for the fatty liver industry should account for body adiposity, a component challenging to measure *in vivo*. To address this, we introduced a TOBEC (Total Body Electrical Conductivity) score to derive RFI2, following the approach of Drouilhet et al. (2014), and also tested a computation without this component. The TOBEC method requires a calibration step to obtain accurate prediction equations from a linear model combining the TOBEC score and the BW of the animal. A previous study had shown that prediction equations existing for rabbits (Fortun-Lamothe et al., 2002) are not applicable to mule ducks (Cornuez et al., 2013). However, no reference was available to recompute prediction equations for our animals, which belonged to three different populations. Consequently, we directly incorporated the TOBEC score into the multiple regression model to compute RFI_2. In both parental lines, RFI_1 and RFI_2 exhibited similar heritabilities and very high genetic correlations (above 0.9). It should be noted, however, that the TOBEC score exhibited different heritabilities in the two parental populations (0.07 ± 0.08 in the Muscovy population and 0.38 ± 0.08 in the Pekin population). This may explain why heritabilites of the two RFI indicators differ more in the Pekin line. Further research is needed to determine the best methods for measuring body composition on farms, with ultrasonic measurements and tomography being potential options, each with varying accuracy and constraints (Grandhaye et al., 2019). Some body measurements have also been suggested to estimate the body composition, including fat content in Pekin (Lin et al., 2018) or Muscovy duck (Kleczek et al., 2006) but are quite tedious and too time-consuming to be routinely implemented in breeding programs.

Comparison of performances between populations

The age difference between lines (Muscovy ducks being tested a week later than Pekin ducks) does not allow for a complete comparison between line traits since young animals are expected to eat less, have lower ADG and have better efficiency. However, although Muscovy ducks (older) had larger ADG than Pekin ducks (younger), they also had lower average daily feed intake, leading to lower FCR values in the Muscovy line compared to the Pekin line, despite the age difference. This is consistent with Muscovy ducks having a leaner meat than Pekin (Larzul et al., 2006; Kokoszyński et al., 2021), especially as foie gras Pekins are fatter than lean Pekins reared for meat. In our study, the observed difference could have been reinforced by studying only males in the Muscovy population, which are generally bigger and leaner than females (Tai and Rouvier, 1998), whereas both sexes were analysed in the Pekin line. Indeed, in their study on a limited number of male ducks measured from day 28 to day 49 (about 40 per line) from lines differing with our study, Cobo et al. (2022) reported larger ADG in a Muscovy line, but not a significantly different average daily feed intake, which also led to lower FCR in Muscovy than in Pekin. Concerning feeding behaviour, this latter study also reported longer feeding times and more feeding events in Muscovy compared to Pekin, with a reduced feeding quantity per event, resulting in much faster feeding rates in Pekin. Finally, the greater similarity between Pekin and mule ducks, compared to Muscovy and mule ducks, in terms of average meal duration and daily feeding time has already been previously reported by Cobo et al. (2022).

Purebred feeding trait genetic parameters

The genetic parameter estimates for feeding behaviour traits in this study were consistent with those obtained on Pekin broilers by Le Mignon et al. (2017) and Thiele (2016). Our heritability estimate for DFI slightly exceeded that reported by Zhang et al (2017) between day 15 and day 42 (0.33 ± 0.11). Several patterns can be drawn from the correlations between feeding traits, with some common features with Le Mignon et al. (2017). First, strong negative genetic correlations between ANM and AMFI indicated that an increase in meal number strongly reduces feed intake per meal. Second, moderately negative correlations of AFR with ANM and AMD suggested that birds exhibiting a high feeding rate may reach satiety quickly, resulting in shorter meals, and less frequent initiation of feeding sequences. Third, an exploitable plasticity in feeding behaviours was emphasised by a large and positive correlation between average meal duration and daily feeding time, which was significantly different from unity. As expected, the latter was also strongly negatively correlated with the feeding rate. These three points were common to both parental populations, suggesting some generalities about duck feeding behaviours, despite the divergence between *Anas platyrhynchos* and *Cairina moschata* that occurred around 14 million years ago (Jiang et al., 2021).

Purebred efficiency trait genetic parameters

In our study, FCR was more heritable than in the two Pekin lines studied by Le Mignon et al. (2017), who reported heritability estimates of 0.24 and 0.31. In the Pekin line, our estimates of the correlation between FCR and feeding behaviour traits aligned with those reported by Thiele (2016) and Le Mignon et al. (2017): except for average daily feed intake, they were of low magnitude (< 0.20). Conversely, in the Muscovy line, FCR was strongly correlated with average feed intake, regardless of the scale, which may suggest a larger variability of FCR due to feed intake compared to the Pekin line. Additionally, in the Muscovy line, ANM and FCR were negatively correlated (-0.5 ± 0.21), indicating that selecting an increased number of meals could improve (i.e., decrease) FCR. This finding contrasts with the literature, which generally associates lower feeding activity with more efficient animals. For instance, Marie-Etancelin et al. (2019) found a positive genetic correlation between the number of daily visits and residual feed intake in Romane sheep, meaning that efficient animals (with a low RFI) would start fewer feeding sequences than less efficient ones. Similarly, Young et al. (2011) estimated a significantly positive phenotypic correlation between RFI and the number of visits in pigs. The significantly positive genetic correlation between AFR and RFI_2 in the Pekin population differs from previously reported findings in pigs, where low RFI animals ate significantly faster than high RFI pigs, suggesting a negative correlation between RFI and feeding rate (Meunier-Salaün et al., 2014).

In conclusion, feeding behaviour traits in parental populations exhibit exploitable genetic correlations with feed efficiency that are likely to facilitate the selection. However, it is crucial to also consider their correlations with the economic traits measured in the mule progeny.

Genetic parameters for crossbred traits

Consistent with Lo et al. (1997), Marie-Etancelin et al. (2011) calculated a pseudo-heritability for crossbred traits as $h^2 = 2(\sigma_s^2 + \sigma_d^2)/(\sigma_s^2 + \sigma_d^2 + \sigma_\varepsilon^2)$, which equates to twice the sum of the parental contributions. As they acknowledged, this pseudo-heritability holds no significance for mule ducks due to the hybrid's sterility. Besides, sire contributions should not be considered as a quarter of the heritability, as would be the case in a homogeneous population. In the context of an intergeneric hybrid between two populations that diverged millions of years ago, where additivity is questionable and both pathways are expected to contribute differently to hybrid traits, such an assumption would lead to misestimations and could result in pseudo-heritabilites outside the parameter space. Based on the estimates presented in Table 5, this would lead to a pseudo heritability of 1.04 for ADFI, 0.9 for AMFI or 0.86 for ANM. For this reason, it is more appropriate to report parental contribution ratios rather than pseudo-heritabilities. In addition to the hybrid specificities, it is accepted that the dam contribution encompasses more than purely additive effects, unlike the sire contribution, and may, therefore, be overestimated.

Genetic parameters for slaughter traits

The estimated genetic parameters of mule slaughter traits confirm a common precept in the fatty liver industry that holds that "the Muscovy sire brings the liver while the Pekin dam brings the meat" and, consequently, the well-documented antagonism between liver and meat weights (Marie-Etancelin et al., 2009, 2011). In this regard, it may be noted that the Muscovy parental contribution to thigh weight is not significantly different from zero and is similar to that found by Marie-Etancelin et al. (2011).

For liver weight, sire and dam contributions were of similar magnitude, while the sire contribution only halved the dam one for skinned breast muscle and thigh weights. This revealed a proportionally larger contribution from the sire to liver weight. The antagonism between meat and liver weights was stronger in the Muscovy population. Marie-Etancelin et al. (2011) reported similar findings in the common duck population (contributions of 0.15, 0.32 and 0.20 for liver, skinned *magret* and thigh weights, respectively, as well as negative correlations between liver weight and meat traits, and a positive correlation between skinned *magret* and thigh weights). In this paper, contributions were also lower in the Muscovy population (0.08, 0.07 and 0.05 for liver, skinned breast muscle and thigh weights, respectively). Our estimates for liver melting rate parental contributions and genetic correlation with liver weight align with their results. These genetic correlations are further supported by a phenotypic correlation of -0.83 estimated between liver weight and technological yield, which is one minus the melting rate (Bonnefont et al., 2019).

Relationship between feed efficiency proxies and slaughter traits

The low correlation observed between average daily gain and liver weight in both pathways, as previously reported by Chapuis and Larzul (2006) and Marie-Etancelin et al. (2008), confirms that improving liver weight through selection cannot rely solely on the growth performance of selection candidates. In both parental lines, the genetic correlation of FCR with the slaughter traits of mule offspring was clearly positive (hence unfavourable) with liver weight, and negative with the meat traits (skinned *magret* and thigh weights). This agreed with results previously reported after selection for improved feed efficiency (i.e., a reduced FCR) that increased the proportion of lean tissues, as observed in rabbits (Molette et al., 2016) and in pigs (Gilbert et al., 2017; Young and Dekkers, 2012).

More generally, RFI tended to have lower genetic correlations with slaughter traits than FCR, underscoring the advantage of RFI in describing the portion of feed intake that is not influenced by maintenance and production requirements. However, in the Muscovy population, unlike the Pekin population, significant correlations were still observed between RFI traits and slaughter traits.

Finally, the high correlation of RFI_2 with slaughter traits found in the Muscovy population suggests that finer *in vivo* proxies of the body adiposity would be key to improving the feed efficiency of growing animals without impairing their ability to sire progeny with desirable slaughter performances.

Relationship between feeding behaviour and slaughter traits

Liver and skinned breast muscle weights are significantly related to feeding behaviour traits in both parental lines. To improve liver weight using feeding behaviour traits, selection in the dam pathway should focus on increasing ADFT and decreasing the average feeding rate, favouring birds that spend more time feeding. In the sire pathway, an improved liver weight is expected to result from a selection for a reduced meal number and an increased meal duration. However, increasing meal duration may reduce breast meat weight due to antagonistic genetic correlations, while reducing the number of meals may increase technological loss after cooking.

To improve *magret* and thigh weights, the Pekin population could be selected for an increased feeding time, regardless of the scale, with no detrimental effect on liver weight. It is also worth noting that the above-mentioned feeding behaviour traits were obtained at ages (7 weeks in Pekin and 8 weeks in Muscovy) compatible with the selection stages commonly used in breeding schemes, so no adjustment of the test periods is required.

Consequences for the selection of the parental populations of the mule duck

For a long time, the maternal pathway of the mule duck (i.e., the Pekin population) has been selected for improved laying performances, with an emphasis on plumage colour in the 1990 s (Marie-Etancelin et al., 2008). Progeny tests have also been used for improvement of foie gras production, but are difficult to implement in this pathway because only males are overfed according to current practices. Consequently, the number of mule offspring available for accurately estimating a Pekin dam's genetic merit for foie gras production is limited. In the sire pathway, selection for improved feed efficiency has been proposed, often relying on the performances of mule half-siblings reared in pens (Drouilhet et al., 2014). However, the introduction of automatic feeders has significantly changed the selection process in both sire and dam pathways. Now, selection candidates can be assessed based on traits such as daily feeding time and feeding rate in the dam pathway, or meal duration and number of meals in the sire pathway, which exhibit non-zero correlations with key traits like liver weight and liver melting rate. This reinforces the benefits of joint models that combine purebred and crossbred performances to enhance selection accuracy through multitrait genetic evaluation. However, due to multiple unfavourable correlations, further research is required to accurately determine the optimal weights for an index that combines traits measured on purebred candidates and mule siblings. This index should aim to simultaneously improve feed efficiency and slaughter performance in mule ducks. Nevertheless, in the dam pathway, moderate genetic correlations between RFI and both liver and meat traits provide opportunity for selecting feed efficiency without adverse effects on slaughter traits. Additionally, improving feed efficiency in the parental populations by reducing FCR or RFI is likely to pay off in the mule population since correlations between purebred and crossbred traits are favourable, even if they are different from unity.

Conclusion

As demonstrated by the genetic analyses conducted on a large experimental design, feeding behaviour traits, which are non-lethal, are heritable. Both feed efficiency traits in the parental lines and slaughter traits in the mule ducks show exploitable correlations with these feeding behaviour characteristics. Thanks to electronic feeders, selection indexes for foie gras production can now be enhanced by incorporating new non-lethal traits, measured on selection candidates. These traits exhibit significant genetic correlations with key economic components such as foie gras weight, *magret* weight and technological yield. Consequently, improved efficiency in the selection for improved foie gras and *magret* production is anticipated. The new selection indexes should, however, also account for melting rate and the mule duck feed efficiency, despite the presence of unfavourable genetic correlations.

Supplementary material

Supplementary material to this article can be found online at https://doi.org/10.1016/j.animal.2024.101234.

Ethics approval

The present study was conducted in agreement with the 2010/63/EU regulation for the use of animals for research purposes. Animals were bred at the INRAE Palmiped farming system facility (AVIPOLE, Benquet, France), which has been approved for animal experimentation (C40-037-1). Experiments were carried out following a protocol approved by the French Ministry of Higher Education, Research and Innovation, in accordance with European regulations for animal care (APAFIS# 13467-2018013116519672v7).

Data and model availability statement

The data and script samples have been deposited in an official repository and are available at https://doi.org/10.57745/DA0EQD. Information can be made available from the authors upon request.

Declaration of Generative AI and AI-assisted technologies in the writing process

During the preparation of this work the author(s) did not use any AI and AI-assisted technologies.

Author ORCIDs

H. Chapuis: https://orcid.org/0009-0003-6841-7160.
CMD. Bonnefont: https://orcid.org/0000-0002-7521-4754.
I **David:** https://orcid.org/0000-0002-2514-6693.
A. Hazard: https://orcid.org/0000-0003-0997-6432.
H. Gilbert: https://orcid.org/0000-0002-4385-3228.

CRediT authorship contribution statement

H. Chapuis: Writing – original draft, Project administration, Funding acquisition, Formal analysis, Conceptualization. **M. Lagüe:** Resources. **CMD. Bonnefont:** Writing – review & editing, Data curation. **I. David:** Writing – review & editing, Methodology. **M.-D. Bernadet:** Resources. **A. Hazard:** Writing – review & editing, Resources. **H. Gilbert:** Writing – review & editing, Supervision.

Declaration of interest

The authors declare no conflict of interest.

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