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► **To cite this version:**

Parsaoran Silalahi. Experimental evaluation of the effects of selection on reproductive and robustness traits in a Large White pig population. Animal biology. Université Paris Saclay (COMUE), 2017. English. NNT : 2017SACLA009 . tel-01627083

HAL Id: tel-01627083

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NNT : 2017SACLA009

THESE DE DOCTORAT
DE
L'UNIVERSITE PARIS-SACLAY
PREPAREE A
AGROPARISTECH (INSTITUT DES SCIENCES ET INDUSTRIES DU VIVANT ET
DE L'ENVIRONNEMENT)

ECOLE DOCTORALE N°581
Agriculture, alimentation, biologie, environnement et santé
Spécialité de doctorat : Génétique Animale

Par

M. Parsaoran Silalahi

Evaluation expérimentale des effets de la sélection sur des caractères de reproduction et de robustesse dans une population de porcs Large White

Thèse présentée et soutenue à Paris, le 28 Février 2017 :

Composition du Jury :

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Résumé

Silalahi, P. 2017. Evaluation expérimentale des effets de la sélection sur les caractères de reproduction et de robustesse dans une population de porcs Large White.

Des améliorations importantes ont été obtenues dans les populations porcines pour les caractères inclus dans l'objectif de sélection, i.e. la croissance, l'efficacité alimentaire, la composition de la carcasse et, dans les lignées maternelles, la prolificité des truies. Cependant, la sélection affecte potentiellement un nombre beaucoup plus grand de caractères génétiquement corrélés avec l'objectif de sélection. En effet, les évolutions favorables mentionnées ci-dessus ont été accompagnées d'effets négatifs sur un certain nombre d'autres caractères économiquement importants. Les animaux sélectionnés pour une efficacité productive élevée peuvent avoir une sensibilité accrue aux problèmes comportementaux, physiologiques ou immunologiques, i.e. être moins robustes. Ces effets négatifs de la sélection sont souvent difficiles à mettre en évidence, car les caractères correspondants ne sont pas mesurés de façon systématique dans les programmes de sélection. Comme l'a suggéré Smith (1977), l'utilisation de semence congelée apparaît comme une méthode élégante pour estimer les évolutions génétiques pour un grand nombre de caractères (habituellement non enregistrés). Son principe est d'utiliser la semence congelée pour produire des animaux représentatifs de la population au début du processus de sélection et de les comparer à un échantillon représentatif de la population après sélection. Chez le porc, un stock de semence congelée de verrats Large White français nés (LW) en 1977 et collectés à la fin des années 1970 a été utilisé deux décennies plus tard pour évaluer les évolutions génétiques pour un grand nombre de caractères. Deux groupes expérimentaux (L77 et L98) ont été produits en inséminant des truies LW nées en 1997-1998 avec, soit la semence congelée des verrats LW de 1977 mentionnés ci-dessus, soit la semence fraîche de verrats nés en 1998. Le LW a été principalement sélectionné pour accroître l'efficacité de la croissance des tissus maigres et la prolificité des truies au cours de la période 1977-1998, de sorte que les différences entre les 2 groupes estimées dans cette étude reflètent principalement des réponses directes et corrélées à la sélection sur ces 2 composantes. Quinze verrats non apparentés et 90 femelles de chacun des groupes L77 et L98 ont été choisis au hasard comme reproducteurs et maintenus pour produire jusqu'à 6 portées successives. Les données produites par ces porcs reproducteurs L77 et L98 et leurs descendants (porcs G77 et G98) ont été le support de cette thèse.

La première étude a porté principalement sur les composantes de la carrière reproductive des truies. Les effets de la sélection sur le développement de la maturité sexuelle ont été estimés dans les deux sexes. Ils se sont avérés relativement limités, sauf pour le taux d'ovulation à la puberté, qui a

fortement augmenté chez les cochettes L98 en comparaison des L77 (+3.6 ; $P < 0.001$). L'analyse des données de reproduction jusqu'à la mise bas montre que la sélection a entraîné une forte amélioration de la productivité numérique et pondérale de la truie à la naissance. Les truies L98 «modernes» peuvent conduire jusqu'à la mise bas des portées beaucoup plus nombreuses et plus lourdes (6.8 porcelets/truie/an et 10.4 kg/truie/an). L'augmentation du nombre de porcelets est associée à une réponse corrélative importante sur le taux d'ovulation, qui excède largement l'augmentation de la taille de la portée. Le gain en nés totaux a également été accompagné d'une augmentation corrélative du nombre de porcelets nés vivants, mais aux dépens d'une augmentation du nombre de mort nés. Même si l'augmentation du nombre de porcelets nés est intéressante au plan économique, l'évolution de la mortinatalité n'est pas souhaitée par les éleveurs, ni plus globalement par la société, pour des considérations évidentes de bien-être animal. Cette amélioration de la taille de portée a également été accompagnée de réponses corrélatives défavorables pour d'autres caractères, tels que la variabilité résiduelle de la taille et du poids de portée au cours de la carrière de la truie. La plus grande variance de la taille de portée à la naissance ne résulte pas d'une variabilité accrue du taux d'ovulation, mais plutôt de l'expression complète de la variabilité de la capacité utérine chez les truies L98. Chez les truies L77, la variabilité de la capacité utérine serait limitée par le taux d'ovulation dans une plus grande proportion de femelles. Cette variabilité accrue indique une plus grande sensibilité à l'environnement, qui pourrait être interprétée comme une robustesse réduite des truies L98. Enfin, l'expérience a mis en évidence une diminution assez forte de la longévité des truies. Cette longévité plus faible des truies L98 a réduit de 35% leur avantage sur les truies L77 en termes de production totale de porcelets au cours de la vie de la truie. Cette évolution défavorable a pu apparaître en race pure dans la mesure où la longévité n'est pas un objectif majeur dans les noyaux de sélection, dans lesquels des intervalles de génération courts sont nécessaires pour optimiser le progrès génétique, mais ne semble pas être présente chez les truies croisées au niveau commercial.

La deuxième étude était consacrée à l'analyse des performances des truies et des porcelets pendant la période d'allaitement. Afin de dissocier autant que possible les effets de la sélection sur les caractères des truies et des porcelets, il a été décidé de mettre en place un dispositif factoriel en échangeant, lorsque cela était possible, la moitié des portées entre les truies L77 et L98. Il a en outre été suggéré d'essayer d'homogénéiser les portées à 7 ou 13 porcelets afin d'avoir des portées à faible ou à forte concurrence entre les porcelets. Les adoptions ont été réalisées avec une bonne efficacité, puisque 156 des 249 portées nourries par les truies L77, soit 63%, étaient des portées mixtes. Les chiffres correspondants pour L98 étaient 143 portées sur 278, c'est-à-dire 51%. Dans ces portées mixtes, 43% des porcelets G77 et 41% des porcelets G98 étaient des porcelets adoptés. Du fait des

adoptions croisées et de la standardisation des portées, la taille et le poids des portées étaient nettement différents de ce qu'elles auraient été sans adoption. Ils ne représentent donc pas la capacité des truies L98 à conserver des portées plus grandes jusqu'au sevrage, mais permettent de comparer les capacités des truies L77 et L98 à nourrir des portées équivalentes, indépendamment du génotype de la portée. L'utilisation d'un dispositif factoriel 2 x 2 et l'homogénéisation de la taille de portée entre les deux groupes expérimentaux a permis de montrer que la sélection a principalement affecté les effets génétiques maternels, alors que les effets génétiques directs (des porcelets) sur la croissance avant le sevrage sont restés inchangés. L'évolution des effets génétiques maternels étaient négative, en particulier pour ADG21d et IW21d, qui correspondent à une période où les porcelets dépendent entièrement de la disponibilité du lait de la truie, ce qui signifie que les truies L98 avaient un potentiel inférieur à fournir de l'énergie du lait à leur portée en réponse à une sollicitation donnée de leurs porcelets. Comme les compositions du colostrum et du lait n'ont pas changé au cours des 21 années étudiées, cela signifie que les truies L98 ont une production laitière réduite par rapport à leurs homologues L77. L'augmentation de la variabilité du poids des porcelets à la naissance dans les portées L98 a probablement contribué à la probabilité accrue de mortalité des porcelets G98, en particulier le premier jour après mise bas. En effet, bien que plus lourdes en moyenne, les portées L98 avaient des porcelets plus hétérogènes de sorte que, même si le poids et la proportion de petits porcelets sont similaires dans les portées L98 et L77, les petits porcelets G98 devaient faire face à une compétition accrue à la mamelle en raison de portées plus grandes et de congénères de portée plus lourds, qui conduisait à un risque accru de mortalité par rapport aux porcelets G77. Un autre résultat notable est l'existence d'une plus grande hétérogénéité de croissance des porcelets nourris par les truies L98 comparativement aux truies L77, bien que les adoptions croisées aient éliminé la plus grande partie de la variabilité entre les groupes expérimentaux le 1^{er} jour de lactation. Cela signifie que les truies L98 ont non seulement un effet négatif sur la croissance moyenne des porcelets, mais aussi sur l'homogénéité des porcelets qu'elles nourrissent.

Les résultats des deux premiers chapitres ont montré que la sélection dans la population Large white française a permis une amélioration importante de la productivité numérique et du poids de la truie à la naissance, mais s'est également accompagnée d'une variabilité accrue des performances des truies au cours de la mise bas et de la lactation. Ces résultats ont donc poussé à examiner si les effets de la sélection observés au sevrage n'affectaient pas la croissance après sevrage et les caractères de carcasse. En effet, cela permettrait d'avoir une vue complète quant aux évolutions de la variabilité des performances des porcs à l'engrais tout au long de leur vie. L'objectif de ce 3^{ème} chapitre était d'étudier si la sélection peut affecter la variabilité de la croissance après sevrage et les

performances de la carcasse et si cette évolution peut être attribuée à des changements dans la distribution des poids à la naissance ou au sevrage. Les résultats ont montré que la sélection a conduit à une augmentation de la variabilité de la croissance post-sevrage jusqu'à l'abattage et du poids d'abattage. À l'inverse, l'augmentation de la teneur en viande maigre de la carcasse a entraîné une diminution de la variabilité des caractères d'adiposité et de la teneur estimée en viande maigre de la carcasse. Ces résultats ont des effets défavorables pour les éleveurs, qui auront des difficultés croissantes à avoir tous leurs porcs dans la gamme de poids la plus favorable, en particulier en cas d'une conduite en bandes, ainsi que pour les transformateurs, car une plus grande variabilité du poids à l'abattage est susceptible d'augmenter les coûts de transformation. Nos résultats tendent également à montrer que cette plus grande variabilité de la croissance n'est pas seulement liée à un effet d'échelle. De plus, nous avons montré que la variabilité plus élevée après sevrage n'est pas une conséquence directe de l'augmentation de la variabilité à la naissance, puisque les variabilités avant et après sevrage sont très faiblement corrélées. Nous avons également montré que la sélection a légèrement modifié les corrélations résiduelles entre les caractères, avec une tendance à des valeurs absolues plus grandes dans le groupe G98.

Les origines potentielles de ces corrélations plus fortes ont été étudiées dans le 4^{ème} chapitre, dans lequel nous avons quantifié l'influence des effets macro-environnementaux de la truie sur les performances de ses descendants et examiné si la sélection pouvait avoir changé l'ampleur de ces effets. Les résultats ont confirmé l'impact de certaines caractéristiques de la truie sur les performances de leurs descendants. Cette influence ne se limite pas à la période pré-sevrage, mais peut affecter la croissance des porcs jusqu'à l'abattage et même les performances de carcasse. L'impact plus important est sans aucun doute l'effet négatif de la taille de la portée sur la croissance des descendants pendant les périodes pré- et post-sevrage. La durée de gestation avait des effets positifs sur les caractères de croissance, sauf pour ADGSL chez les truies L98. Les effets de l'âge à la première mise bas ont également évolué entre les G77 et les G98, avec un effet négatif sur la croissance chez les G77 et une tendance positive chez les G98. Une différence significative entre les groupes expérimentaux a également été observée pour AGEPUB. Les coefficients de régression étaient positifs chez les G98, alors qu'ils étaient proches de zéro chez les G77. Ces études ont globalement montré que le dispositif expérimental était adapté pour estimer avec précision les évolutions génétiques dans la population de porcs LW. Dans cette thèse, les caractères de reproduction mâle et femelle et les caractères liés à la robustesse ont été étudiés. Des évolutions fortement favorables ainsi que quelques effets indésirables de la sélection ont été mis en évidence, complétant ainsi les résultats des études précédentes. Cependant, si le dispositif expérimental est approprié pour mesurer les effets cumulatifs de la sélection sur une durée longue, il donne des

résultats de façon assez tardive et ne fournit aucune indication sur la forme des évolutions génétiques au cours de la période considérée. L'estimation des évolutions génétiques à l'aide de la méthodologie du BLUP ("Best Linear Unbiased Prédiction") est plus flexible pour obtenir des informations sur les évolutions génétiques à court terme et de façon régulière. Toutefois, ces évolutions sont dans la plupart des cas limitées aux caractères de l'objectif de sélection ou à ceux utilisés comme critères de sélection. La situation est susceptible d'évoluer à l'avenir avec le développement du phénotypage automatisé et à haut débit, qui peut permettre d'estimer les évolutions génétiques pour un beaucoup plus grand nombre de caractères.

Le dispositif expérimental analysé dans cette thèse a pris fin il y a dix ans. Les objectifs de sélection au cours de la période considérée ont évolué dans le temps, mais portaient principalement sur les caractéristiques de production, i.e. la vitesse de croissance, l'efficacité alimentaire, la teneur en viande maigre, la qualité de la viande et, pendant les années 1990, la prolificité des truies. Ces dernières années, des caractères supplémentaires ont été ajoutés à l'objectif de sélection de la population Large White française. Ces modifications dans l'objectif de sélection ont conduit à des changements supplémentaires dans la population LW. Il serait intéressant de compléter l'étude actuelle par une estimation des évolutions génétiques plus récentes à l'aide du BLUP en utilisant des données en ferme.

Enfin, cette étude a montré que deux décennies de sélection ont donné lieu à un progrès génétique important pour des caractères d'intérêt majeur, mais qu'elles ont également affecté des caractères tels que la longévité, le risque de mortalité, la variabilité des caractères, qui tendent à indiquer un effet défavorable de la sélection sur la robustesse des porcs. Nos résultats soulignent la nécessité d'intégrer des traits liés à la robustesse dans l'objectif de reproduction des populations porcines. Dans un contexte commercial pratique, la sélection pour la robustesse doit être envisagée de façon équilibrée avec celle des caractères de production. C'est déjà en partie le cas pour certains caractères, i.e. la longévité ou la survie, qui ont été intégrés dans l'objectif de sélection de certaines populations porcines, mais cela reste un défi pour les caractères liés à la sensibilité environnementale ou à la santé. Plusieurs auteurs ont proposé de sélectionner les animaux sur la base de leurs normes de réaction ou de caractères liés à la robustesse comme des caractères de résistance aux maladies, de réponse immunitaire ou de faire une meilleure utilisation de la diversité génétique, qui peut permettre de produire des animaux mieux à même à faire face à la variabilité de l'environnement. La sélection génomique présente un intérêt certain, car elle permet de sélectionner des porcs plus robustes sur la base d'informations de marqueurs ou de gènes et de limiter le phénotypage de caractères souvent difficiles à mesurer à la population de référence. Ainsi, de nouvelles recherches sont nécessaires pour mieux caractériser les différentes composantes de la

robustesse et leur impact sur l'efficacité, le bien-être et la santé des porcs afin de pouvoir définir les objectifs d'élevage les plus pertinents pour l'avenir.

Mots clés : *porc, semence congelée, évolution génétique, reproduction, robustesse, croissance des porcelets, survie des porcelets, poids à la naissance, caractères de carcasse, variabilité de la croissance, caractéristiques de la truie.*

Summary

Silalahi, P. 2017. Experimental evaluation of the effects of selection on reproductive and robustness traits in a Large White pig population.

Large improvements have been obtained in major pig populations for traits included in the breeding goal, i.e. growth, feed efficiency, carcass composition and, in maternal lines, sow prolificacy. However, selection potentially affects a much larger number of traits which are genetically correlated with the breeding goal. Indeed, the above-mentioned favorable trends have been accompanied by adverse effects on some other economically important traits. Animals selected for high production efficiency may in particular be more sensitive to behavioral, physiological, or immunological problems, i.e., be less robust. These adverse effects of selection are often difficult to reveal, as corresponding traits are not routinely recorded in breeding programs. As suggested by Smith (1977), the use of stored frozen semen has been shown to be an elegant method to estimate genetic trends for a large number of (usually not recorded) traits. Its principle is to use the frozen material to produce animals that are representative of the population at the beginning of the selection process and compare them with a representative population sample after selection. In pigs, a stock of frozen semen of French Large White (LW) boars born in 1977 and collected at the end of the 1970s was used 2 decades later to estimate genetic trends for a large number of traits. Two experimental groups (L77 and L98) were produced by inseminating French Large White sows born in 1997-1998 with either stored frozen semen from the above-mentioned 1977 LW boars or with fresh semen from LW boars born in 1998. The Large White population has mainly been selected for lean tissue growth efficiency and sows prolificacy over the 1977–98 period of time, so that the differences between the 2 groups estimated in this study mainly reflect direct and correlated responses to selection on these 2 components. Fifteen unrelated boars and 90 females from each of L77 and L98 experimental groups were randomly chosen and kept to produce up to 6 successive litters. The data produced by these L77 and L98 breeding pigs and their progeny (G77 and G98 pigs) were the support of this thesis.

The first study focused on components of sow lifetime productivity. The effects of selection on the development of sexual maturity were estimated in both sexes. They appeared as rather limited, with the exception of ovulation rate at puberty, which strongly increased in L98 as compared to L77 gilts (+3.6; $P < 0.001$). The analysis of sow reproduction data up to farrowing shows that selection has resulted in large improvements in sow numerical and weight productivity at birth. “Modern” L98 sows are able to carry up to term much larger and heavier litters (6.8 piglets/sow/year and 10.4 kg/sow/year). The increase in the number of piglets is associated with an important correlative

response in ovulation rate, which largely exceeds the increase in litter size. The gain in total born has also been accompanied by a correlative increase in the number of piglets born alive, but at the expense of an increase in the number of stillbirths. Even if the increased number of piglets born is economically interesting, the trend in stillbirths is not desired by farmers, as well as more globally by the society, for obvious animal welfare considerations. This improvement in litter size has been accompanied by unfavorable correlative responses for other traits, such as residual variability of litter size and weight along sow productive life. The larger variance of litter size at birth does not result from an increased variability of ovulation rate but rather from the full expression of the variation in uterine capacity in L98 sows. In L77 sows, uterine capacity variation would be limited by the number of ova shed in a larger proportion of females. This increased variability indicates a higher sensitivity to the environment, which might be interpreted as a reduced robustness of L98 sows. Finally, the experiment showed a rather strong decrease in sow longevity. This impaired longevity of L98 sows reduced by 35% their advantage over L77 sows in terms of lifetime piglet production. This unfavorable trend may have occurred in purebred populations because longevity is not a major objective in purebred lines, in which short generation intervals are required to optimize genetic trends, but does not seem to be present in crossbred sows at the commercial level.

The second study was devoted to the analysis of sow and piglet performance during the nursing period. In order to disentangle, as much as possible, the effects of selection on sow and litter performance, a factorial design was set up by exchanging, when it was possible, half litters between L77 and L98 sows. It was additionally suggested to try to homogenize litters to either 7 or 13 piglets in order to have litters with low or high competition between piglets. Crossfostering was successful, as 156 of the 249 litters nursed by L77 sows, i.e. 63%, were mixed litters. Corresponding figures for L98 were 143 of 278 litters, i.e. 51%. In these mixed litters 43% of G77 and 41% of G98 piglets were crossfostered. Due to crossfostering and litter size standardization, litter size and weights were different from what would have happened without crossfostering. They consequently do not represent the capacity of L98 sows to maintain larger litters until weaning, but rather the comparative abilities of L77 and L98 sows to nurse similar litters, independently from litter genotype. The 2 x 2 factorial design and the homogenization of litter size between the two experimental groups has allowed to show that selection has mainly affected maternal genetic effects, while direct (piglet) genetic effects on pre-weaning growth have remained unchanged. The trend was negative for maternal genetic effects, particularly for ADG21d and IW21d, where piglets entirely depend on sow milk availability, which means that G98 sows had a lower potential to provide milk energy to their litter in response to a given demand from their piglets. As colostrum and milk composition have not changed during these 21 years, it implies that L98 sows had a reduced milk production as compared

to their L77 counterparts. The increased variability in piglet weight at birth in L98 litters could have contributed to the increased probability of mortality of G98 piglets, particularly on d 1. Indeed, though heavier on average, L98 litters contain more heterogeneous piglets so that, even if the weight and proportion of small piglets are similar in L98 and L77, small G98 piglets have to face an increased competition to the udder due to larger litters and heavier littermates, leading to an increased risk of mortality as compared to G77 piglets. Another noticeable result is the existence of a larger heterogeneity in the growth of piglets nursed by L98 sows as compared to L77 sows, although cross-fostering had removed the largest part of the heterogeneity between experimental groups on d 1. This implies that L98 do not only have an unfavorable effect on average piglet growth rate, but also on the homogeneity of the piglets they nurse.

Results from the first two chapters showed that selection in French Large White population has resulted in large improvements of sow numerical and weight productivity at birth. However, it was also accompanied by an increased variability of sow performance during farrowing and lactation. These results consequently encouraged investigating whether the effects of selection observed at weaning affected growth performance after weaning and carcass traits. Indeed, this would allow to have a full picture of trends in the variability of slaughter pig performances during their whole life. The objective of the third chapter was to investigate whether selection affected the variability of post-weaning growth and carcass performances and whether it can be attributed to changes in the distribution of birth or weaning weights. Results showed that selection has led to an increase in the variability of post weaning growth until slaughter and of slaughter weight. Conversely, the improvement of carcass leanness has resulted in a decreased variability of fatness traits and of estimated carcass lean content. These results have some unfavorable impacts for farmers who will have increased difficulties to have all their pigs in the most favorable range of weights, particularly in all in all out systems, as well as for processing units, as a higher variability of body weight at slaughter is likely to increase processing costs. Our results also tended to show that the increased variability of growth traits was not only due to a scale effect. Moreover, we showed that it was not a direct consequence of the increased variability at birth, as pre-weaning and post-weaning variabilities appear as uncorrelated. We also showed that selection has slightly changed residual correlations between traits, with a tendency towards larger absolute values in G98.

The potential origins of these larger correlations were further investigated in the 4th chapter in which we quantified the effects of sow macro-environmental effects on progeny performances and investigated whether selection could have changed the magnitude of these effects. The results confirmed the impact of some sow characteristics on their progeny performance. This influence is not limited to the pre-weaning period, but can affect piglet growth until slaughter and even carcass

performances. The most important impact was undoubtedly the negative effect of litter size on progeny growth during the pre- and post-weaning periods. Gestation length had positive effects on growth traits, except for ADGSL in G98 sows. The effect of age at first farrowing changed between G77 and G98, with a negative effect on growth traits in G77 and G98 and a tendency towards positive effects in G98. A significant difference between experimental groups was also observed for age at puberty. Regression coefficients were positive in G98, while they were close to zero in G77.

These studies globally showed that the design was suitable to accurately estimate genetic trends in French Large White Pig population. Within this thesis, male and female reproduction as well as robustness related traits were investigated. Strong positive effects and some undesired effects of selection were shown, complementing the results of previous studies. However, if this experimental design was suitable to measure cumulative effects of selection after a long period of selection, it gives rather late trends and does not provide any indication on the shape of genetic trends during the period considered. Estimating genetic trends with best linear unbiased prediction (BLUP) is more flexible to get short term and regular information on genetic trends. However, they are in most cases limited to the small number of traits considered in the breeding goal or as selection criteria. The situation is likely to change in the future with the development of automatized, high density phenotyping, which will make it possible to estimate genetic trends for a much larger number of traits.

The experimental design analyzed in this thesis has ended ten years ago. Breeding goals over the period considered evolved over time, but mainly focused on productive traits i.e. growth rate, feed efficiency lean meat content, meat quality and, during the 90's, sow prolificacy. In recent years, additional traits have been added to the breeding goal of French dam pig populations. These modifications in the breeding goal have led to additional changes in the Large White population. It might thus be interesting to complement the current study with more recent BLUP estimates of genetic trends using field data.

Finally, this study has shown that 2 decades of selection have resulted in large gains for major traits of interest, but have also adversely affected traits such as longevity, risk of mortality, trait variability, which tend to indicate an unfavorable effect of selection on pig robustness. Our results stress the necessity to integrate robustness related traits in the breeding goal of pig populations. Additional new criteria related to robustness would be worth considering to avoid further degradation of these traits. In a practical commercial context, selection for robustness traits has to be in balance with selection for production traits. This is already partly the case for some traits, i.e. longevity or survival traits, which have been incorporated to the breeding goal of some pig

populations, but it largely remains a challenge for environmental sensitivity or health related traits. Several authors have proposed to select animals either on the basis of reactions norms or on various robustness related traits such as traits related to the resistance to diseases, to immune response or to make a better use of genetic diversity, which may allow to produce animals that are more prone to cope environment variability. Genomic selection is of high interest, because it allows us to select more robust pig on the basis of marker or gene information and to limit phenotyping of traits that are often difficult to measure to the reference population. Thus, further research is needed to better characterize the different components of robustness and their impact on pig efficiency, welfare and health to be able to define the most relevant breeding objectives for the future.

Keywords: *pig, frozen semen, genetic trend, reproduction, robustness, piglet growth, piglet survival, birth weight, carcass performance, growth traits variability, sow features.*

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General introduction

Major pig populations have been intensively selected over the last decades, leading to considerable improvements in production and reproduction traits (Dourmad et al., 2010; Tribout et al., 2010). Pig selection initially started based on visual appearance then on individual phenotype or progeny means. With advances in computing power, BLUP (Best Linear Unbiased Prediction), which integrates pedigree and performance data of all candidates' relatives, has become the method of choice to select breeding pigs. Recent advances in genomics currently leads to the development of genomic evaluation programmes (Hayes et al., 2013). Each new methodology has increased the overall efficiency of breeding schemes. The traits selected, which define the breeding goal have also evolved over time, moving from the above-mentioned visual appearance to selection for a large number of traits associated with pig lean growth efficiency, pork quality as well as male and females reproductive efficiency (Dekkers et al., 2010).

However, animals selected for high production efficiency may be more sensitive to behavioural, physiological, or immunological problems (Rauw et al., 1998; Phocas et al., 2014; Rauw and Gomez-Raya, 2015; Prunier et al., 2010). Sows with large litter sizes need more resources to supply litter demand. Feed intake is restricted by the size of the animal and the biochemical processes involved in nutrient uptake and utilization. Undesired effects of selection have been observed in several pig populations such as an increasing number of stillbirths (Canario et al., 2007b; Lund et al., 2002), changes in maternal abilities (Canario et al., 2014b), increasing leg problems or sensitivity to environment.

These undesired effects of selection may have been enlarged by changes in production conditions associated with new rules (e.g. limitation of the use of antibiotics in pig feed), changes in both the perception of livestock production and consumption preferences by citizens / consumers. Moreover, climate change likely has put additional constraints on the environment the animals have to face. Selecting pigs which are able to face these changing conditions and perform well in a variety of situations is a formidable challenge for animal breeders. A lot of research is currently developed to increase livestock adaptive capacities and robustness. Robustness is often defined as the capacity of an animal to maintain a high production level in a variety of environments without impaired health, reproduction and welfare (Knap, 2005). Robust pigs are required to perform well in presence of various stressors or variable environmental conditions.

These adverse effects of selection are often difficult to reveal, as the corresponding traits are not routinely recorded in breeding programs. The use of frozen semen is an efficient way to measure genetic trends for a large number of usually not recorded traits. It is thus of particular interest to reveal potential unfavourable effects of selection. The general objectives of this thesis are to investigate the effects of selection on reproductive traits, with a special attention given to robustness related traits, by using frozen semen.

The thesis is structured in three main parts:

- The first part is a literature review on genetic improvement in pigs and on potential undesired effects of selection.
- The second part presents the results of an experimental estimation of genetic trends in French Large White population from 1977 until 1998, subdivided into four parts.
- The third and last part is a general discussion of the results obtained, with a special emphasis on robustness, and of potential strategies to improve robustness in pig populations.

1. – Evaluation of the efficiency of breeding schemes

Breeding schemes are often relatively complex structures that, in competitive markets, have both short (stay on the market) and long term (maximize genetic progress) targets. Their efficiency should be regularly monitored, both to ensure that realized trends for target traits are in line with expectations based on predicted genetic changes and that the breeding process does not result in deterioration of other traits, either because they have unfavorable genetic relationships with traits from the breeding goal or because of genetic drift. Realized genetic trends may indeed differ from the predictions due to inadequate data description models, errors in the genetic parameters used, choices or uses of the breeding stock that do not exactly correspond to the breeding goal. The aim of this first chapter is to briefly describe the structure and functioning of a pig breeding scheme, to present available methods for controlling genetic trends, to provide information on the breeding history of the population investigated in this thesis, i.e. the French Large White population and describe traits that will receive a special attention in this thesis.

1.1. - Organisation of pig breeding schemes

1.1.1. Some elements on pig production

Pigs are mostly exploited for meat production, which is either consumed as fresh meat or as processed products. There are a wide variety of processed products (dry or cooked hams, bacon, roast pork and sausages) for which different qualities may be desired. Some productions are associated with specific breeds / genetic types, such as the Iberian pig in Spain or, on a much smaller scale, Basque or Gascon pigs in France. Such examples, however, remain an exception: the vast majority of pig farming aims at producing a standardized product (pigs of 5 to 6 months of age slaughtered at an average live weight of 100 to 120 kg) to provide consumers with rather inexpensive and good quality fresh meat and processing units with raw materials for processed products. The biological variability of this material is often used by slaughterhouses to sort carcasses and carcass cuts according to the desired characteristics for a particular type of processed product. In many countries, the pig industry is a rather integrated chain involving several actors or partners, i.e. breeding organizations, feed factories, pig production, slaughterhouses, processing units, retail outlets and pork consumers.

Pig production is structured around two main activities: weaner activity, which aims at producing young piglets (around 25-35 kg live weight), and grower activity aiming at raising pigs from 25 kg to slaughter at 100-120 kg live weight. These activities can be carried out in a single weaner/grower herd or in specialized weaner and grower herds. Different sets of traits contribute to the efficiency for each activity. For weaners, the main objective is to produce a large number of piglets with a good growth potential, so that increasing sow numerical productivity (P_N), i.e. the number of piglets produced per sow per year (e.g. Legault, 1978) - is a major goal. Variations of P_N mainly depend on sow prolificacy (i.e. the total number of piglets born per litter) and piglet survival (Milligan et al., 2001a). Other traits, such as the regularity of rebreeding after weaning, the length of productive life, maternal behaviour at farrowing and during the suckling period, sow autonomy (ease of farrowing, ...) which determine farmers' amount of work, as well as health traits, are also important concerns. On the male side, boar libido, the quantitative and qualitative aspects of semen production, as well as the length of productive life, which is strongly related to the boar's ability to maintain a satisfactory semen production over time, are also important features.

The efficiency of grower activity has two main determinants, i.e. pork value and (lean) growth efficiency. Pork value depends on carcass weight and lean content, which directly affect pig selling price, and on meat quality. Growth efficiency is a function of growth rate and of feed efficiency, which additionally contributes to reduce manure production and GHG emission, and the cost of pig health, which determines mortality rates until slaughter and may indirectly affect production traits. Meat quality includes a complex set of traits including processing, eating, nutritional and hygienic qualities. A large number of traits are associated with these different qualities (Sellier, 1998; Ciobanu et al., 2011), including the post mortem evolution of pH, colour, drip loss, intramuscular fat content, firmness, juiciness, flavour, technological or cooking loss, fatty acid composition, fibre characteristics as well as boar taint, a meat quality defect that is likely to appear in meat from entire males. Boar taint is essentially due to 2 major components, skatole and androstenone, the latter being a steroid, which may hence be related to male and female reproductive traits. Most piglets are currently castrated shortly after birth to avoid boar taint, which raises growing societal concerns about welfare. Farmers are not paid for meat quality in standard production systems, but may be penalized in case of meat quality defects such as boar taint or low meat ultimate pH.

1.1.2. Pig breeding goals and breeding programmes

Breeding can largely contribute to increase the efficiency of pig production. An essential step to reach pig breeding goal is to properly define a breeding objective or breeding goals (Dekkers et al., 2010). A breeding goal is a (usually) linear combination of the traits to be improved, i.e.:

$$H = w_1 A_1 + w_2 A_2 + \dots + w_n A_n$$

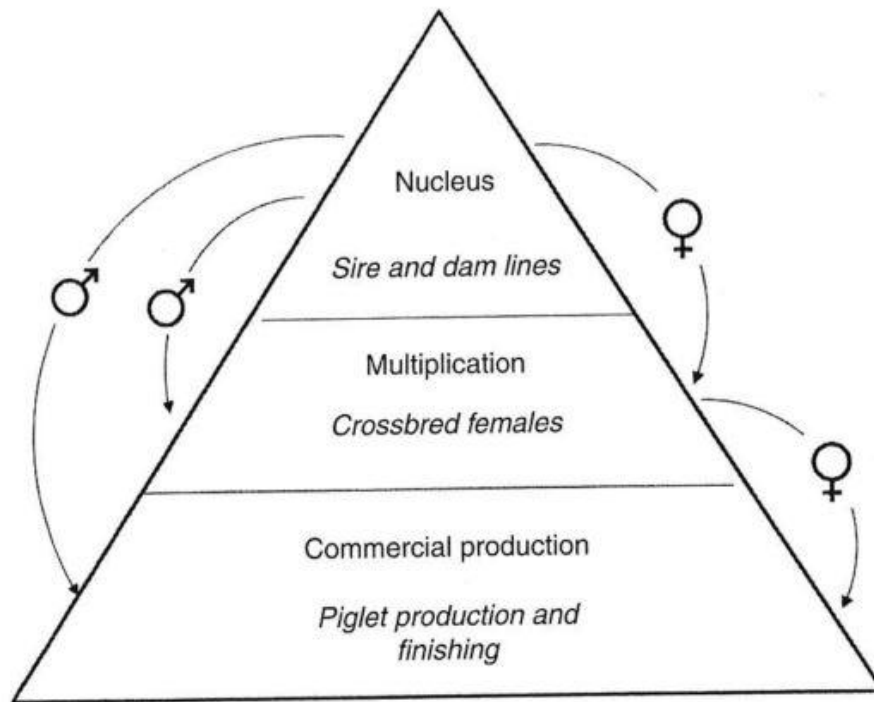
where A_1, A_2, \dots, A_n are breeding value of the traits to be selected and w_1, w_2, \dots, w_n are the relative weights of each trait, often referred to as “economic” weights. These weights can be determined in different ways. The most widely used method is to derive weights from more or less complex profit functions (PF). It is computed for each trait x_i as the partial derivative of PF with regard to x_i ($\partial PF / \partial x_i$) or, in other words, as the variation of PF due to a given change (e.g. a fraction of a phenotypic standard deviation) in that trait, holding all others traits constant (De vries, 1989a; Olesen et al., 2000; Quinton et al., 2006; Amer et al., 2014). Another frequently used technique is the so-called « desired gain » method. Its principle is to find the weight leading to a desired genetic trend predicted from relevant methods derived from the breeder’s equation and accounting for overlapping generations, Bulmer effect, ... Available softwares such as OPTIPIG (Maignel et al., 1997), SelAction (Rutten et al., 2002) or Zplan+ (Täubert et al., 2010) are often used for such studies. Other methods to derive such weights can be found in the literature, such as using of biological functions (Fowler et al., 1976), accounting for competitive position (De Vries, 1989b) or including non-monetary objectives (Kanis et al., 2005), but will not be detailed here.

Selection is a cumulative and long-term process, so that breeding goals should not be changed too often. Yet, economic conditions, consumer and social demands evolve other time, so that breeding goals must be regularly re-evaluated to see whether they are still in line with future needs. For instance, over last decades, pig breeding objectives first aimed at improving the performance and carcass traits of growing pigs, have then included meat quality and sow prolificacy in dam lines, then maternal abilities and are now considering to include traits related to robustness, i.e., a reduced general sensitivity to pathogens or, more generally to variations in environmental conditions. Due to increasing societal concern, traits related to animal welfare and environmental footprint of production will probably have to be considered in future breeding goals.

Genetically, the above-mentioned standardization is facilitated using a limited number of genetic types issued from crosses between lines belonging to a limited number of internationally exploited breeds or populations (see below). Crossbreeding is indeed an important component of pig breeding schemes. Its use is made easier by the pyramidal structure of pig breeding programs. Selection is performed in a small number of farms called nucleus herds, which are managed under high health and biosecurity levels to reduce the risk of diseases that may endanger purebred populations and limit the marketability of breeding pigs. The best animals are kept to generate the next generation. The best among the remaining animals are sent to multiplication herds, whose function is to provide many improved animals to commercial farms. On the male pathway, the use of

artificial insemination may to some extent allow the use of the best boars at both nucleus and multiplication or production levels (figure 1.1).

Figure 1.1. Pyramidal structure of pig breeding programs



This pyramidal structure is well suited to the use of crossbreeding, which allows to take advantage of heterosis effects on several traits of economic interest (reproduction, growth, feed efficiency). The most commonly used crossbreeding systems in pigs are three or four way-crosses in which females exploited in commercial herds (usually named “parental sows”) are F1 crossbred sows produced at the multiplication level and mated or inseminated by either purebred (3-way cross) or F1 crossbred (4-way cross) “terminal” boars. Purebred populations are called grand-parental populations (GPP) in these two-tier crossbreeding systems. More complex crossbreeding systems exist in pigs, where parental sows or terminal boars are 4-way or 4-way crosses. In this case, purebred breeds/lines are called grand-grand-parental populations (GGPP).

In most cases, the populations used to produce parental sows and terminal boars are different. Breeds and lines exploited for production of parental sows are called dam lines, while those used to produce terminal boars are called paternal lines. The desirable qualities are different in the two types of populations. Production traits, i.e. growth rate, feed efficiency, carcass conformation and quality, meat quality, as well as male reproductive efficiency (libido, semen quality) are prioritized in sire

lines, while a balance between production and female reproductive traits, i.e. litter size, piglet survival, and growth, teat number and longevity, is searched for in dam lines. Crossbreeding between sire and dam lines allows to benefit from the so-called complementarity effect between the two types of populations (e.g. Moav, 1966). The most commonly used dam lines are varieties (i.e. independent sub-populations) of Large White and Landrace breeds, while sire lines are often varieties of Duroc, Piétrain and to a lesser extent, Hampshire breeds. Yet, Large White sire lines and Duroc dam lines have also been developed in some cases. Moreover, most breeding companies have developed specific synthetic lines by crossing two or more parental breeds followed by several generations of *inter se* matings and within-line selection. For instance, several synthetic dam lines have been produced by crossing European breeds to some highly prolific Chinese native breeds such as Meishan and Jiaxing (Bidanel et al., 1991; Zhang et al., 2000; Banville et al., 2015).

1.1.3. Genetic variability of traits of interest

The efficiency of breeding schemes will also depend on the available genetic variability for traits of interest in the selected populations. This genetic variability is usually characterized by trait heritability, which is defined as the ratio of additive genetic to phenotypic variance and indicates how parent's phenotypic superiority is transmitted to their offspring, and by genetic correlations between traits, which determine correlative responses to selection and the easiness to select on multiple traits. Many reviews on the genetic parameters of traits of interest have been published in pigs with, among the most recent ones, chapters from the book "The genetics of the pig", where the genetic variability of reproduction, growth, carcass and meat quality traits have been reviewed by Bidanel, (2011), Ciobanu et al. (2011), Clutter, (2011). We will focus on reproductive traits and their relationships with other traits of interest, which are of particular interest for this thesis.

Heritability values for major female and male reproductive traits are given in table in table 1.1. Except for a limited number of traits which only depend on female genotype, i.e. age at puberty, ovulation rate, weaning to oestrus interval or oestrus behaviour, female reproductive traits have low heritabilities (below 0.20). These low values are partly due to their complexity. Most of them and in particular litter size and weight do not depend only on sow genes, but also on the genotypes of the boar and of the piglets. Most studies have tried to quantify the relative contributions of sow, boar and piglet genotype on the variability of female reproductive traits. The service sire has a rather limited effect on litter size, except in very specific cases such as the presence of chromosomal abnormalities (Tribout et al., 2000), but might significantly impact fertility (Varona and Noguera, 2001). Piglets have been shown to have a limited, but sometimes significant effect on their own

survival (Knol et al., 2002b; Ibanez-Escriche et al., 2009a) and to increasingly influence their growth from birth to weaning (e.g. Roehe, 1999; Solanes et al., 2004; Rosendo et al., 2007b). However, in spite of their low heritability, traits such as prolificacy have a substantial additive genetic variability and can be improved through selection. Some male reproductive traits, which are essentially related to their morphology, have moderate to high heritability values, while others, such as those related to semen production are also lowly heritable (Table 1.1.).

Table 1.1. Heritability of male and female reproductive traits (Bidanel, 2011)

	Traits	No of estimates	Mean h ²	Range
Female traits	Age at puberty	16	0.37	0-0.73
	Oestrus symptoms	3	0.21	0.09-0.29
	Ovulation rate (OR)	18	0.32	0.10-0.59
	Conception rate (CR)	3	0.10	0-0.29
	Prenatal survival rate (PSR)	12	0.15	0-0.23
	Total number born (TNB)	103	0.11	0-0.76
	Number born alive (NBA)	118	0.10	0-0.66
	Number weaned (NW)	54	0.08	0-1.0
	Farrowing survival rate (FSR)	12	0.07	0.03-0.14
	Birth to weaning survival rate (BWSR)	12	0.05	0-0.13
	Farrowing length (FL)	2	0.07	0.05-0.10
	Litter homogeneity at birth	6	0.08	0.03-0.1
	Litter weight at birth	18	0.24	0-0.54
	Birth assistance	2	0.05	0.05
	Litter weight at 21 days	22	0.14	0.07-0.38
	Weaning to oestrus interval	5	0.22	0.11-0.36
	Rebreeding interval	3	0.23	0.03-0.36
Male traits	Testis width	8	0.37	0.02-0.61
	Testis weight	5	0.44	0.24-0.73
	Semen volume	6	0.19	0.14-0.25
	Sperm concentration	6	0.19	0.13-0.26
	Sperm motility	6	0.11	0.06-0.18
	% abnormal sperm	4	0.10	0.06-0.17
	Libido	13	0.15	0.03-0.47

Genetic correlations between female reproductive traits are shown in Table 1.2. Age at puberty is almost independent from the other female reproductive traits. Counting traits, i.e. the numbers of ova shed, of embryos /foetuses, of piglets and birth and at weaning, have positive phenotypic and genetic correlations, even if correlations between ovulation rate and number weaned are very weak. Conversely, correlations between the different survival rates are low (≤ 0.3 in absolute value) and have varying signs, thus indicating a different genetic determinism. Survival rates, which are ratios, have negative correlations with counting traits when they correspond to their denominator (i.e. ovulation rate (OR) with prenatal survival rate (PSR), total number born (TNB) with farrowing survival rate (FSR) and number born alive (NBA) with birth to weaning survival rate (BWSR)) and tend to be positive one when they correspond to their numerator or to strongly related traits: This is the case for prenatal survival, which has strong positive genetic correlation with TNB, NBA and NW (0.42 to 0.55) and, to a lesser extent for BWSR with NW (0.15). Conversely, FSR is almost independent from NBA and NW ($r_g = 0.01$ and -0.01 , respectively).

Average birth weight has negative genetic correlations with litter size and prenatal survival, and weakly positive relationships with farrowing and birth to weaning survival (0.22 and 0.15, respectively). Though this relationship is approximate, as it does not separate direct and maternal components of genetic variability, and relationships may vary across populations, it tends to show that increasing birth weight would not be a very efficient way to increase piglet survival. Improving the homogeneity of within-litter piglet weight at birth has also been proposed to decrease the number of small piglets, which are more prone to die, and of very big piglets, which would be associated with a higher risk of farrowing difficulties. Indeed, positive genetic correlations between within-litter standard deviation of birth weight and pre-weaning mortality have been reported by several authors (e.g. Roehe and Kalm, 2000; Knol et al., 2002a; Huby et al., 2003) and a selection experiment for the homogeneity of birth weight in rabbits showed favourable relative responses for farrowing and birth to weaning survival (Garreau et al., 2008).

Estimates of genetic correlations between female prolificacy and fertility or rebreeding performance are rather scarce in the literature. Available estimates of the genetic correlation between litter size at birth and weaning to service interval are close to zero (Hanenberg et al., 2001; Imboonta et al., 2007; Lundgren et al., 2010). Yet, as pointed out by Bidanel, (2011), even if there is little evidence of antagonistic relationships between performance and fertility in pigs, such an antagonism is well documented in other species and should hence receive some attention in the future.

Similarly, genetic relationships between female and male reproductive performances are not very well documented. Most studies report low and non-consistent genetic correlations between the two sets of traits (Schinckel et al., 1983; Toelle and Robison, 1985; Young et al., 1986; Johnson et al., 1994). Yet, it should be mentioned that selection for reduced androstenone levels in growing pigs results in a older age at puberty of females (Sellier and Bonneau, 1988).

Table 1.2. Means of literature estimates of genetic (above) and phenotypic correlation (below diagonal) among reproductive traits (Bidanel, 2011)

Traits	AP	OR	PSR	TNB	FSR	NBA	BWSR	NW	LBW	L21W	ABW
AP		-0.06	-0.08	-0.04	-	0.07	-	0.09	-0.10	-0.15	-
OR	0.05		-0.36	0.32	-0.27	0.24	-0.38	0.01	0.24	0.03	-0.23
PSR	-0.01	0.14		0.50	0.3	0.55	-0.25	0.42	0.30	0.10	-0.41
TNB	-0.03	0.13	0.60		-0.25	0.92	-0.15	0.73	0.62	0.40	-0.41
FSR	-	0.06	-0.15	-0.08		0.01	0.17	-0.01	-0.10	0.05	0.22
NBA	-0.03	0.12	0.40	0.91	0.15		-0.14	0.81	0.64	0.55	-0.34
BWSR	-	-0.11	-0.14	-0.12	0.08	-0.22		0.15	-0.07	0.65	0.15
NW	-0.01	0.03	0.36	0.71	0.47	0.79	0.55		0.67	0.81	-0.23
LBW	-0.03	0.07	0.55	0.79	0.43	0.82	0.09	0.71		0.65	0.43
L21W	-0.04	0.02	0.08	0.42	0.36	0.46	0.65	0.80	0.61		0.60
ABW	-	-0.17	-0.32	-0.40	-	-0.44	-	-0.17	0.10	0.07	

AP=age at puberty; OR = ovulation rate; PSR = prenatal survival rate; TNB = total number born; FSR = farrowing survival rate; NBA = number born alive; BWSR = birth to weaning survival rate; NW= number weaned; LBW = litter weight at birth; L21W = litter weight at 21 days of age; ABW= average birth weight.

Production and reproduction traits are often considered as genetically independent in pigs. This was probably true 30 years ago between litter size and growth and carcass traits, as reviewed by Haley et al. (1988). However, as reviewed by Bidanel (2011), the majority of more recent results strongly suggest the existence of low to moderate antagonistic relationships between some production and reproduction traits. Unfavourable genetic correlations were for instance reported between litter size and growth by Ducos and Bidanel, (1996), Hermesch et al. (2000a) and Holm et al. (2004), and between litter size and carcass traits by Zhang et al. (2000), Chen et al. (2003a), Serenius et al. (2004), and Imboonta et al. (2007). Relationships are scarcer and less clear for feed intake and feed efficiency; close to zero correlations were reported by Hermesch et al. (2000a), while a favourable trend for litter size was reported as a correlated response to residual feed intake in growing pigs by Gilbert et al. (2012). With the exception of boar taint, genetic relationships with meat quality traits appear as close to zero in the few available studies (Larzul et al., 1999; Hermesch

et al., 2000b; Serenius et al., 2004; Rosendo et al., 2010). Sexual developments in males and females have favourable genetic correlations with growth and close to zero correlations with carcass and meat quality traits (Bidanel, 2011).

1.1.4. Selection criteria and genetic evaluation

Traits included in the breeding goal can be, but are not necessarily, those who are used to compute the aggregate estimated breeding value (EBV) which is the basis for ranking candidates to selection. Components of this aggregate EBV are selection criteria. For instance, selection for carcass lean content is often based on backfat thickness measurements, which is strongly correlated with carcass lean content and much easier to measure. Selection for feed conversion ratio has been often based on a combination of average daily gain and backfat thickness.

Until the 1990's, pigs have been genetically evaluated using rather simple aggregate EBV computed using selection index methodology (Hazel and Lush, 1942; Hazel, 1943). First indexes were based on progeny testing first developed in Denmark in the beginning of the 20th century. They have then been replaced by indexes based on pigs' own performances or on a combination of own and sib performances. At the end of the 1980's and in the early 1990's, these standard indexes have been replaced by indexes computed using Best Linear Unbiased Prediction (BLUP) methodology (Henderson, 1963; Henderson, 1973) applied to animal models (BLUP-AM). BLUP-AM, which allows to compute estimated breeding values for each pig from the population using the information from all its relatives, and to simultaneously estimate genetic and environmental effects. First applications were implemented in Canada, USA and Denmark for production traits (Ducos et al., 1992). BLUP-AM was of particular interest to select for sow prolificacy, which was very difficult to select on within herd basis (e.g. (Bidanel and Ducos, 1994; Bolet et al., 2001), and to combine on-farm and testing station phenotypic information (Bidanel and Ducos, 1996; Tribout et al., 1998).

Pig has also been one of the first livestock species to use marker assisted selection, then gene assisted selection to get rid of the halothane sensitivity allele in dam lines (Saugere et al., 1989; Amigues et al., 1994) and of the RN- allele in Hampshire based populations (Miller et al., 2000). Apart from these two cases, first generation marker assisted selection based on microsatellite markers has not been widely used in pigs (Dekkers et al., 2010), The availability of the pig genome sequence and of the Porcine Illumina SNP60 BeadChip (Ramos et al., 2009) at the end of the 2000' has resulted in theoretical studies of the genetic and economic interest of genomic selection in pig breeding schemes (Tribout et al., 2012; Tribout et al., 2013; Abell et al., 2014; Lillehammer et al., 2016) and in

the implementation of genomic selection in several pig populations (e.g. Cleveland and Hickey, 2013; Knol et al., 2016; Bouquet et al., 2017).

So far, pig genetic evaluation and selection has mainly been based on phenotypic information collected on purebred pigs in nucleus and multiplication herds. This situation has several advantages and has been successful to increase the performance of commercial crossbred pigs. Yet, it may not be optimal as: 1) it does not consider the partner population used in crossbreeding; 2) it assumes traits have the same genetic determinism in selection and multiplication herds and in commercial herds, i.e. that genetic x environment interactions are limited, which is not totally true. Reciprocal recurrent Selection (RRS), which uses information from the partner population in crossbreeding to select each parental population, allows to benefit from both additive and non-additive genetic effects. RRS is widely used in plant breeding, but has a more limited use in animal breeding (Wei and Van Der Steen, 1991). They may be of interest, but the use of RRS has, to our knowledge, been very limited. Conversely, some breeding schemes use a method which combine information on purebred and on related crossbred animals - combined crossbred purebred selection or CCPS (Wei and van der Werf, 1994). Despite its interest, the use of this method is often limited by the lack or the poor quality of pedigree information on commercial pigs. The use of genomic selection is likely to change the situation, as pedigree information is no longer required. The joint use of crossbred and purebred information in livestock species where crossbreeding is developed (pigs, poultry, ...) is currently a very active research topic (Ibanez-Escriche et al. 2009b; Christensen et al. 2014; Esfandyari et al., 2016).

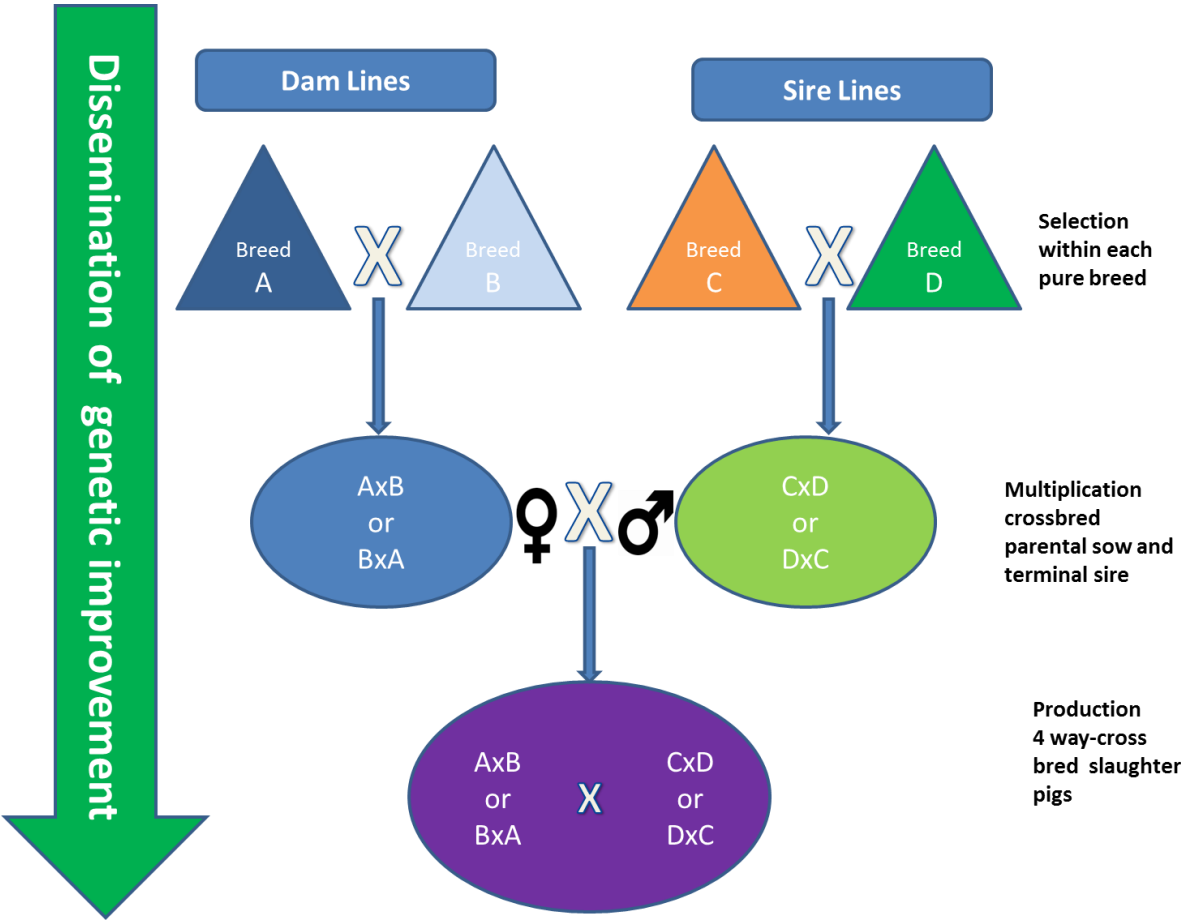
Whatever the method used, the population in which future breeding pigs are chosen is usually limited to a small number of specialized farms whose function is to select candidates, called selection nuclei. The size of these is limited, so most of pig populations are, genetically, of limited size. Pig breeders are faced with problems of management of genetic variability and search for compromise between selection intensity and management of inbreeding. These issues have been studied in detail in paternal and maternal populations (De Roo, 1988; De Vries et al., 1989a).

1.2. Measuring the efficiency of pig breeding schemes

The efficiency of a pyramidal genetic improvement scheme can be considered at different levels. It can be considered at the level of commercial products, which represent the vast majority of pigs and the target animals of the breeding scheme. Yet, this evaluation is very global, and it may be useful to more accurately know the efficiency of each component of the breeding scheme, i.e. the

efficiency of selection in each nucleus herd and of the diffusion of genetic progress from nucleus to commercial herds. It strongly depends on gene flows, which determine how the nucleus herd is replaced by the next generation and how the genetic progress created in nucleus herds is transmitted to the multiplication and commercial levels. Figure 1.2. illustrates the gene flows observed in a typical 4-way crossbreeding scheme.

Figure 1.2. Gene flows in a typical 4-way crossbreeding scheme



1.2.1. Evaluation at commercial level

Evaluations at the commercial level can be based on either large scale data recording systems or on specific experimental designs. Large scale recording systems have been developed in several countries such as G3T (Technical management of sow herds), developed for almost 50 years in France (Legault et al., 1971) or BDporc in Catalonia (e.g. Babot et al., 2003). These large databases provide an accurate picture of performances at the commercial level and are very useful for technical

and economical comparisons in different herds, regions, ... and over time. Though often in line with genetic trends in parental populations, these observed trends are only phenotypic trends. In most cases, such technical databases lack sufficiently reliable pedigree information to accurately dissociate genetic and environmental effects.

An alternative solution is to control representative samples of commercial populations in the same environment. This approach has mainly been used to compare commercial products from different breeding schemes. It has been used in France to compare the production performances of commercial pigs from approved breeding schemes in the frame of the terminal products evaluation (Anonymous, 2009). It has also been used in Quebec (Hammell et al., 1993) and in the USA as part of the maternal line national genetic evaluation program (Serenius et al., 2006). The repeated use of these designs over time makes it possible, under certain assumptions, to compare the relative efficiency of different selection schemes over time.

1.2.2. Evaluation of genetic trends in Nucleus herds

The efficiency of breeding schemes at the nucleus level is most often evaluated by estimating genetic trends in each purebred population. The main difficulty in estimating genetic trends is to distinguish between genetic and environmental trends. A variety of methods to estimate genetic trends can be found in the literature. Some of them are based on the use of an unselected control population reared under the same environment as the selected population, others make use of pedigree information to disentangle genetic from environmental trends. Others based on repeated matings or repeated sires (Goodwin et al., 1955) have been used in pigs (e.g. Canon et al., 1992), but will not be detailed as they have no longer been used since the generalisation of BLUP methodology for genetic evaluation.

1.2.2.1. Use of a control population

The first and the simplest method to estimate genetic trends is the use of an unselected control population issued from the same base population. As described in figure 3, population means at time t can be written as:

$$\bar{\mu}_{S,t} = \mu + g_{S,t} + E_{S,t} + e_{S,t}$$

$$\bar{\mu}_{C,t} = \mu + g_{C,t} + E_{C,t} + e_{C,t}$$

where μ is the general mean of the base population, $\bar{\mu}_{X,t}$, $g_{X,t}$, $E_{X,t}$ and $e_{X,t}$ are the observed mean, the change in mean breeding value, the change in mean environment and the error in estimating the mean breeding value for population X (X = S or C for Selected and Control populations, respectively). The expected value of $e_{X,t}$, $E(e_{X,t})$ is 0 in all cases. If the environment similarly affects the two populations, i.e. if there is no population x environment interaction, $E(E_{S,t} - E_{C,t}) = 0$ and the expected genetic trend at time t (ΔG_t) is equal to the difference between observed means at time t :

$$\Delta G_t = E(\bar{\mu}_{S,t} - \bar{\mu}_{C,t}) = E(g_{S,t}) - E(g_{C,t})$$

Yet, using such an approach requires to control and minimize the effects of factors that can decrease accuracy or bias estimates of genetic trends. A decreased accuracy can result from an error in the estimation of the means ($\bar{\mu}_{S,t}$ and $\bar{\mu}_{C,t}$) due to the limited number of animals recorded, and from genetic drift, a random variation in allelic frequencies due the limited size of the populations. The drift variance accumulates over generations and can be predicted from the number of breeding animals and the way they are chosen and used (Sellier, 1980). Genetic drift in population X (X = S or C) is equal to :

$$Var(\bar{\mu}_{X,t}) = 2F_{X,t}\sigma_A^2$$

Where F_t is the average inbreeding coefficient of population X at time t. F_t can be expressed as (Falconer and Mackay, 1996):

$$F_t = 1 - (1 - \Delta F)^t = 1 - \left(1 - \frac{1}{2N}\right)^t$$

where N is the effective size of population X, which can be expressed as a function of the number of breeding males and females and of the mating strategy. If F_t is low, the drift variance can be approximated as (Hill, 1980; Falconer and Mackay, 1996):

$$Var(\bar{\mu}_{X,t}) \cong t \frac{\sigma_A^2}{N}$$

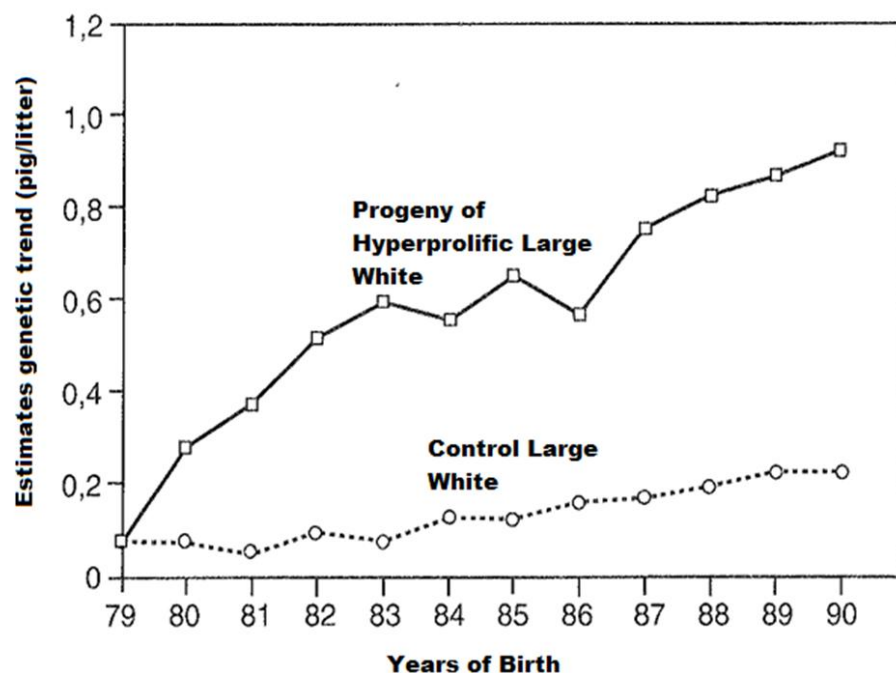
The variance of response to selection can easily be derived from population drift variance. For instance, in a short term selection experiment with a control line can be approximated as (Hill, 1980) :

$$Var(\bar{\mu}_{S,t} - \bar{\mu}_{C,t}) \cong \left[t \left(\frac{1}{N_S} + \frac{1}{N_C} \right) + \left(\frac{1}{M_{S,0}} + \frac{1}{M_{C,0}} \right) \right] \sigma_A^2 = (tA + B_0)\sigma_A^2$$

where σ_A^2 is the additive genetic variance, t is the number of generations, $M_{X,0}$ and $N_{X,0}$ (X = S or C) are the numbers of individuals sampled and the effective population size in S and C, respectively.

Biases in the estimation of genetic trend can result from natural selection, inbreeding depression and genotype x environment interactions (Sellier, 1980). Natural selection cannot be avoided, but it is likely to be limited in carefully managed populations if the period of time considered is not too long. Inbreeding depression is also a source of bias, as it decreases the mean population performance, but it remains limited at low levels of inbreeding. If population x environment interactions are present, then $E(E_{S,t} - E_{C,t}) \neq 0$, so that $E(\bar{\mu}_{S,t} - \bar{\mu}_{C,t})$ is no longer an unbiased estimation of genetic trend.

Figure 1.3. Genetic evolution of 'Hyperprolific large white compared to standard large white (Bidanel and Ducos 1994)



1.2.2.2. Use of frozen material (semen or embryos)

Provided that it is technically feasible, the use of frozen semen or embryos is a rather convenient method to measure genetic trends in both experimental and commercial populations. Its principle is to freeze material from a selected population SP and, after some time, to re-implant the frozen embryos or to use the frozen semen to produce a new population whose performances are compared with those of a random sample of the SP population. Theoretical aspects of the use of frozen material to estimate genetic trends was studied by Smith (1977), who compared the relative interest of a discontinuous (D : the frozen material is used once after several years) vs a continuous

(C : the frozen material is used every year) use of frozen material. Using frozen semen, he estimated annual genetic trend ΔG_a as (under the assumption of no genotype environment x interaction) :

D approach:
$$\Delta G_a = 2 (\bar{\mu}_{SP,t} - \bar{\mu}_{FC,t})/t$$

C approach:
$$\Delta G_a = 2 \bar{b}_{SP-FC,t}$$

where, $\bar{\mu}_{SP,t}$, $\bar{\mu}_{FC,t}$ are the mean performances of the selected and of the frozen control populations at time t, respectively, and $\bar{b}_{SP-FC,t}$ is the linear regression on time of the differences measured at different periods of time. This linearity assumption can be relaxed if the trend clearly appears as non-linear. The discontinuous approach appeared as more accurate for a given number of animals phenotyped, but does not give any information on the shape of genetic trend during the period considered.

Smith (1977) also discussed the advantages and problems of these approaches as compared to a standard control line. Main advantages are the absence of genetic drift and inbreeding over many generations, the adaptation of these approaches to both experimental and field populations, the possibility to estimate genetic trends for additional, previously unrecorded, traits and the limited cost of producing and maintaining germplasm pools. As compared to BLUP genetic estimation of genetic trends, they also have the advantage of not depending from genetic parameter estimates. On the other hand, biases may arise from:

- potential long-term effects of freezing or storage, such as epigenetic modifications;
- direct or indirect effects on viability or performance; for instance, the size of embryo transferred litters or even of litters produced from frozen semen cannot be compared with litters produced from fresh semen. One way to avoid or at least limit this bias would be to freeze semen or embryos from the selected population before using them. If litter size widely differs between the frozen control and the selected population, this difference may indirectly affect the progeny performance for traits that are influenced by litter size mediated maternal effects; a standardisation of litter size at birth or the production of a second generation are possible ways to limit this potential source of bias;
- after a long period of time, gene frequencies may have significantly changed in the selected population, so that the population issued from frozen semen could exhibit some heterosis effects; if such a case, the production of a second generation would divide by half the amount of heterosis effects;

- The number and the choice of individuals to produce frozen material are of major importance; this is particularly true for frozen embryos: as the success rate is still limited, a large number of embryos originating from many sires and dams is required. The choice of sires is of particularly importance for both embryo and semen production, as semen is likely to be obtained from artificial insemination boars, which are a selected sample of the initial population. In that case, the sires used to produce the animals from the selected population should have the same superiority over the selected population as frozen semen boars.

This approach, more precisely the use of frozen embryos, has been used in rabbits to estimate genetic trends after 21 generations of selection for litter size (Garcia and Baselga, 2002). In France, semen from French Landrace and Large White boars born in 1977 was frozen and stored at the end of the 1970's. Experiments were set up to estimate genetic trends for production and meat quality traits in the two breeds after 5, 10 and 20 years of selection, respectively (Molénat et al., 1986; Ollivier et al., 1991; Bazin et al., 2003). A parallel experiment was set up after 20 years of selection to estimate genetic trends for a larger number of traits in the Large White breed and is the basis of this thesis (see later).

1.2.2.3. Use of Best linear unbiased prediction (BLUP) methodology

Best Linear Unbiased Prediction (BLUP) has been the most widely used methodology to estimate breeding values over the last 25 years. BLUP is Best in the sense that it is the Predictor which minimizes the prediction error variance (and maximizes the correlation between true and predicted breeding values) in the class of Linear (it is a linear combination of observations) Unbiased (i.e. its expectation is equal to the true values of the parameters) predictors. Its main advantage over standard selection indexes lies in the fact that it allows to simultaneously account for all pedigree information and environment effects in the estimation of breeding values. BLUP animal model estimates of breeding values (BLUP-BV) have several other desirable properties. First, BLUP-BV have been shown to be unbiased by selection, provided that the model used to describe the data is correct, that the true genetic parameters are being used and that it includes all the data on which selection decisions were based since the beginning of the selection process (Henderson, 1975; Sorensen and Kennedy, 1984). Under these same assumptions, BLUP-BV remain unbiased when replacing true genetic parameters by their restricted maximum likelihood estimates (e.g. Gianola et al., 1989; Juga and Thompson, 1989) and BLUP-AM accounts for genetic drift, assortative mating and inbreeding (Sorensen and Kennedy, 1983). Finally, BLUP animal models easily provide estimates of genetic trends, which are computed as changes in average BLUP-BV over time. For instance, yearly

genetic trends can be obtained at any moment by computing average BLUP-BV according to animals' year of birth. BLUP-AM is thus a formidable tool which potentially allows an almost real-time control of the efficiency of selection in selected populations. Things may be somewhat less simple in real situations, as the above-mentioned assumptions of data exhaustiveness may not be fulfilled, which may result in potential biases due to errors in genetic parameter estimates and an incomplete description of the selection process. Moreover, genetic trends can be obtained only for traits that are regularly measured during the period considered.

1.3. Genetic trends in pigs

The objective of this third part of chapter on is to provide results on estimated genetic trends (EGT) in the population investigated, i.e. French Large White dam breed, in order:

- to put the experiment analyzed in this thesis in its context,
- to analyze the consistency of the results obtained in this experiment with other estimates of genetic trend in this same Large White population,
- to compare the results obtained in Large White breed to available literature results in other populations.

An additional objective will be to present and discuss potential adverse effects of selection in order to identify traits which should receive a particular attention.

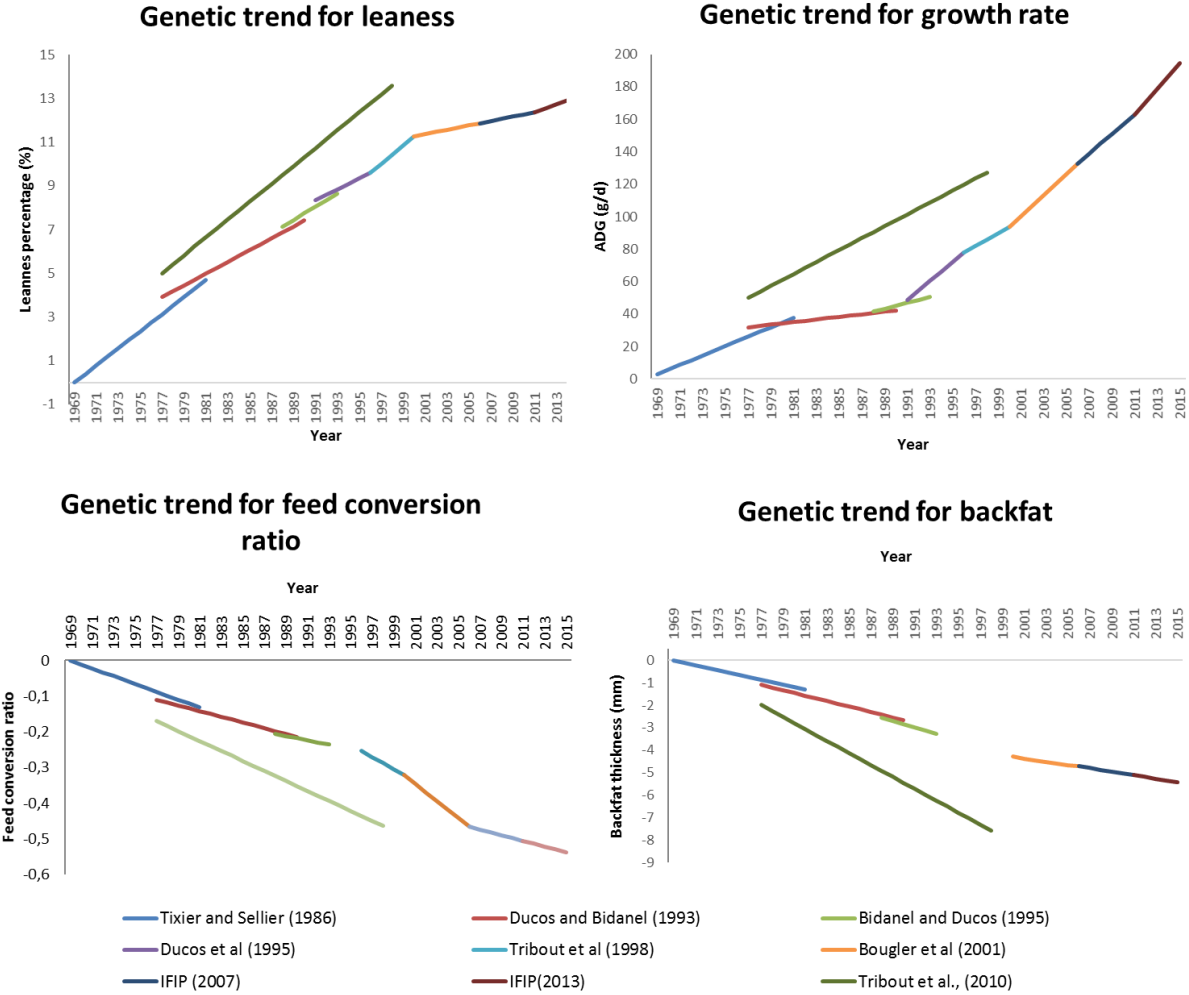
1.3.1. Estimates of genetic trends in pig populations

As mentioned above, several results of the current experiment have already been published. Yet, most of them (Canario et al., 2007a; Canario et al., 2007b; Foury et al., 2009; Canario et al., 2014b) concern traits that were not previously measured, and thus cannot be compared. In fact, the results obtained on standard production traits (Tribout et al., 2010) are the only traits that can be compared with either BLUP estimates of genetic changes or with results from previous experiments based on the use of frozen semen (Molénat et al., 1986; Ollivier et al., 1991; Bazin et al., 2003).

BLUP genetic trends estimated over successive periods of time for 4 major production traits have been compiled and compared with those obtained by Tribout et al (2010) in figure 1.4. Trends from both methods are rather consistent, except for average backfat thickness where a larger trend is obtained by Tribout et al (2010) as compared with BLUP estimates.

The situation is less consistent when comparing the results of Tribout et al (2010) with previous estimates based on frozen semen (table 1.3). Differences are particularly important with the results of Molénat et al. (1986) and, to a lesser extent, Ollivier et al. (1991), who report surprisingly large estimated genetic trends. As discussed by Ollivier et al. (1991), these results are likely to be overestimated due to a strong disequilibrium in sire progeny size, to the limited period of time considered and to changes in the breeding goal, with the successive introduction of meat quality (1980's) and litter size (1990's) in the breeding goal. The results are more consistent with those reported by Bazin et al. (2003) during the same time interval (1977-1998) as Tribout et al. (2010), except for growth rate, and, to a lesser extent food conversion ratio. In spite of these differences, it can be argued that the current experiment provides rather relevant estimates of genetic trends and can be used to measure genetic trends for a larger number of traits.

Figure 1.4. Comparison of BLUP and frozen semen estimates of genetic trends



Estimates have also been compared with those published in other populations in different countries, mainly Europe and America. Results are shown in table 1.4 and 1.5 for production and reproduction traits, respectively. It should be pointed out that most estimates from the scientific literature are rather old, i.e. from the 1990's, and that the recent results have been obtained from technical reports. They are mainly originating from "national" organisations, as most private breeding companies do not publish their results, presumably for fear of unfavourable comparisons with competitors. Large variations are observed between breeds, the moment and the length of the period considered. They reflect differences in breeding goals over time and between populations, as well as potential differences in selection efficiency. Average genetic trends are 6.4%, -7.1%, -5.7% and -5.8% of trait phenotypic standard deviation for average daily gain, feed conversion ratio, average backfat thickness and carcass lean content, respectively. Recent estimates tend to be larger than old ones, indicating an increased efficiency of selection. The majority of estimates in French populations exceed the above-mentioned average values, even in dam lines. Average trends for reproduction traits are 0.11 (total number born), 0.12 (number born alive), 0.10 (number weaned) and 0.06 (teat number). Genetic trends in French populations have been limited until the mid-nineties and the inclusion of litter size in the breeding goal of Large White (LW) and Landrace (LR) populations. Since 1995, annual trends have been 0.23 and 0.17 piglet born alive/litter, respectively, in LW and LR breeds.

Table 1.3. BLUP estimates of annual genetic trends for production traits

Reference	Breed ¹	Period of time	Trait ²				
			ADG (g/d)	FCR	ABT (mm)	LEAN%	MQI
(Molénat et al., 1986)	LW	1977-1982	-24.5	-0.09	-1.10	0.93	-0.04
	LR	1977-1982	14.8	-0,01	-0.26	0.19	-0.25
(Ollivier et al., 1991)	LW	1977-1987	12.8	-0.032	-0.50	0.36	-0.04
	LR	1977-1987	13.9	-0.022	-0.27	-0.19	-0.02
(Bazin et al., 2003)	LW	1977-1998	9.1	-0.019	-0.24	0.32	0.04
	LR	1977-1998	5.8	-0.005	-0.13	0.23	-0.21
(Tribout et al., 2010)	LW	1977-1998	3.7	-0.014	-0.25	0.41	-

¹LW = Large White; LR = Landrace.

²ADG = average daily gain on test, age at 100 kg or Days to 113 kg; FCR = feed conversion ratio or efficiency; ABT=Average backfat thickness; LEAN% = carcass lean content or lean to fat ratio or % of valuable cuts; MQI=meat quality index.

Table 1.4. BLUP estimates of annual genetic trends for production traits in foreign pig populations (*results are expressed in % of within-breed phenotypic standard deviation*)

Reference	Breed ¹	Period of time	Trait ²			
			GROW TH	FCR	ABT	LEAN %
(Hudson and Kennedy, 1985)	LW	1974-1982	-2.8		-5.1	
	LR	1974-1982	-3.4		-6.4	
	HA	1974-1982	-2.6		-2.3	
	DU	1974-1982	-1.3		-2.4	
(Tixier and Sellier, 1986)	LW	1969-1981	3.5	-4.8	-14.0	13.5
	LR	1969-1981	1.3	-3.5	-8.9	4.8
(Kovac and Groeneveld, 1990)	LW	1979-1987	6.1	-5.6		-1.0
	LR	1979-1987	2.8	-2.6		-17.6
	PI	1979-1987	7.4	-8.6		-4.2
(Hofer et al., 1992)	LW	1976-1987	1.5			9.8
	LR	1976-1987	2.4			6.5
(Ducos and Bidanel, 1993)	LW	1977-1990	0.9	-3.6	-6.2	6.6
	LR	1977-1990	2.8	-3.8	-5.2	5.5
(Bidanel and Ducos, 1995)	PI	1978-1993	2.8	-3.0	-3.4	7.8
(Ducos et al., 1995)	LW	1989-1993	1.9	-2.6	-9.9	7.5
	LR	1989-1993	5.9	-4.3	-7.1	7.9
(Tribout et al., 1998)	LW-D	1991-1996	5.8		-12.7	10.4
	LR	1991-1996	5		-9.9	8.9
	LW-S	1991-1996	9.2		-10.3	7.2
	DU	1991-1996	7.6		-13.0	10.7
(Chen et al., 2002)	LW	1990-2000	-3.1		-12.7	10.4
	LR	1990-2000	-3.8		-9.9	8.9
	HA	1990-2000	-1.0		-10.3	7.2
	DU	1990-2000	-4.3		-13.0	10.7
(Habier et al., 2009)	PI	1985-2003	1.6	-5.0		8.1
	LW	2007-2013	-6.3	-4.8	-1.1	0.0
(Canadian Centre for Swine Improvement, 2014)	LR	2007-2013	-4.8	-3.0	0.0	-0.3
	DU	2007-2013	-10.0	-7.0	-4.7	1.6
(IFIP - Institut du Porc, 2016)	LW-D	2001-2006	8.6	-3.5	-4.7	5.8
	LR	2001-2006	7.1	-7.8	-8.8	0.6
	LW-S	2001-2006	5.8	-9.6	-3.5	3.5
	PI	2001-2006	7.1	-11.4	-8.9	7.5
(Danbred, 2016)	LW	2011-2014	12.7	-11.3		1.0
	LR	2011-2014	9.7	-12.9		1.6
	DU	2011-2014	20.6	-16.0		4.8

¹LW = Large White or Yorkshire; LR = Landrace; HA = Hampshire; DU = Duroc; PI = Piétrain ; -D = dam line; -S = sire line.

²GROWTH = average daily gain on test, age at 100 kg or Days to 113 kg; FCR = feed conversion ratio or efficiency; ABT= average backfat thickness; LEAN% = carcass lean content or lean to fat ratio or % of valuable cuts.

Table 1.5. BLUP estimates of annual genetic trends for some reproduction traits in pigs (*results are expressed in trait units*)

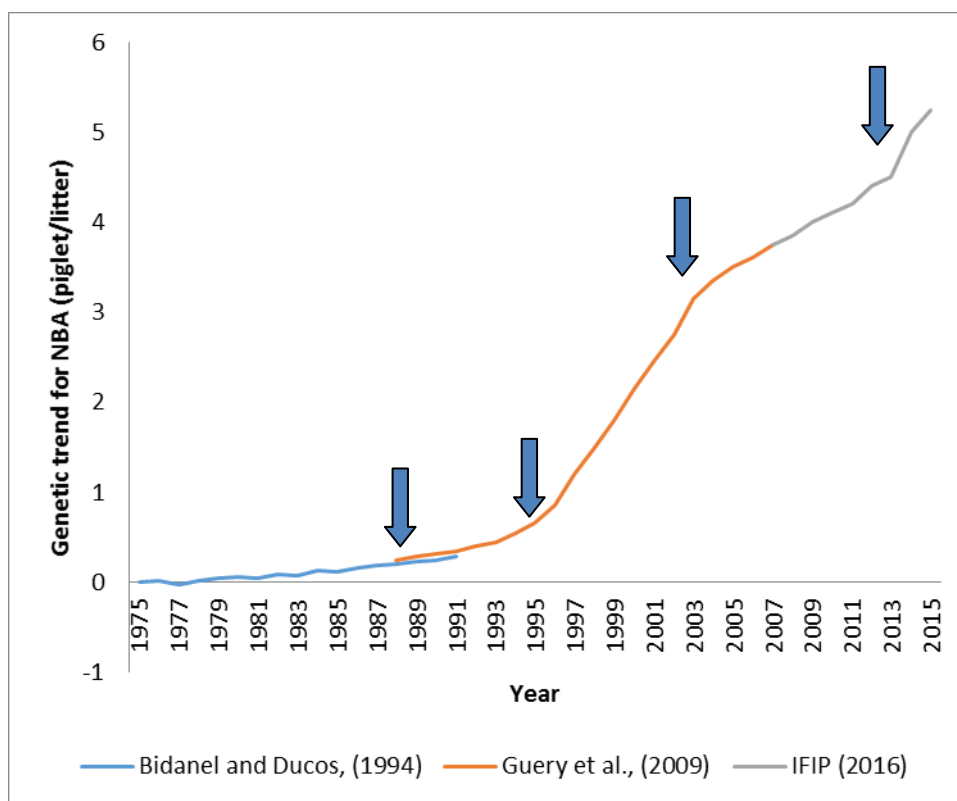
Reference	Breed ¹	Period of time	Trait ²				
			TNB	%SP	NBA	NW	TEAT
(Ferraz and Johnson, 1993)	LW,LR	1987-1991			0.01		
(Bidanel and Ducos, 1994)	LW	1975-1991			0.02		
	LR	1975-1991			0.01		
(Guéry et al., 2009)	LW	1988-1996	0.15		0.10	0.08	-
		1996-2002	0.29		0.34	0.24	-0.03
		2002-2007	-0.01		0.14	0.13	0.16
	LR	1988-1996	0.12		0.08	0.05	-
		1996-2002	0.28		0.26	0.22	0.05
		2002-2007	0.01		0.05	0.04	0.16
(IFIP - Institut du Porc, 2013)	LW	2008-2013			0.09	0.11	0.16
		2013-2015			0.38	0.26	0.10
	LR	2008-2013			0.12	0.09	0.13
		2013-2015			0.23	0.18	0.07
(Chen et al., 2003b)	LW	1984-1999			0.03	0.01	
	LR	1984-1999			0.02	0.00	
	HA	1984-1999			0.01	0.00	
	DU	1984-1999			0.01	0.00	
(Barbosa et al., 2010)	LW	1996-2006	0.02				
(Tomiyaama et al., 2011)	LW				0.16		
(Canadian Centre for Swine Improvement, 2014)	LW	2007-2013	0.11	0.28			0.02
	LR	2007-2013	0.14	0.33			0.02
	DU	2007-2013	0	0.05			0.02
(Danbred, 2016)	LW	2011-2014			0.21		
	LR	2011-2014			0.16		

¹ LW = Large White or Yorkshire; LR = Landrace; HA = Hampshire; DU = Duroc.

²TNB = Total Number born; %SP = Percentage of piglet survival at birth; NBA= Number born alive; NW = number weaned; TEAT =Teat number

Yet trends have not been linear (see figure 1.5.). After a steep increase until 2002, accompanied by an important degradation of piglet survival at birth, it was decided to change total number born in the breeding goal by a combination of number born alive and teat number. Both traits have increased until 2013, but at a lower rate than in the previous decade. In 2013, competition with Danish and Dutch population has led French breeding organisations to increase the economic weight of number born alive and decrease that of teat number, resulting in a large increase in NBA from 2013-2015. The 1977-1998 period considered in this study thus corresponds to beginning of the increase in prolificacy.

Figure 1.5. Estimated genetic trend for number born alive in French Large White breed



1.3.2. Undesired effects of selection

Production levels in pigs have considerably increased over last decades as a result of both selections, the generalisation of crossbreeding and improved management practices. As mentioned above, selection does not only affect selected traits, but also a much larger number of traits genetically correlated to the traits of the breeding goal. Correlated trends can be favourable - e.g. selection for feed efficiency results in decreased nitrogen and phosphorus excretion (Shirali et al., 2012; Saintilan et al., 2013) -, but is also sometimes detrimental. For instance, including the total

number of piglets born in the breeding goal of pig dam lines has often resulted in an increase in the number of stillbirths in nucleus herds (Canario et al., 2006b; Su et al., 2007; Silalahi et al., 2016) as well as at the commercial level (see table 1.6.). The objective of this chapter is to review potentially undesirable effects of selection on major economically important traits.

Table 1.6. Phenotypic trends in French commercial herds (Prunier et al., 2010)

Traits	1986	1996	2006
Growth rate between 35 -115 kg live weight (g/d)	676	740	770
Percentage of lean tissue	-	59.9	61.5
Total number born	11.1	11.9	13.8
Number born alive	10.5	11.1	12.7
Number of piglet weaned	9.1	9.7	10.8
Percentage of stillbirth (%)	5.4	6.7	8.0
Pre weaning mortality (%)	13.3	12.6	14.4
Total piglet loss (%)	17.6	18.3	21.0
Age at weaning, days	27.4	26.9	24.9
Farrowing Interval, days	155.8	152.4	148.7

1.3.2.1. Piglet survival

The detrimental effects of selection for the total number of piglets born per litter (TNB) on the number (NSB) and the proportion of stillbirths (SB%) is well documented. Most estimates of genetic correlations between TNB and NSB or SB% are positive (Johnson et al., 1999a; Lund et al., 2002) and several studies have reported unfavourable correlative responses to selection for TNB (Ruiz-Flores and Johnson, 2001; Canario et al., 2007b; Guéry et al., 2009). This increased number of stillborn has been shown to be associated with prolonged birth intervals (van Rens and van der Lende, 2004; Vallet et al., 2010), with differences in sow behaviour at farrowing (Canario et al., 2014b) and could involve differences in uterus contractions.

Selection for litter size has also increased the number of small piglets in the litter, which cannot compete with bigger piglets for the best teats and have a lower survival probability (Quiniou et al., 2002; Milligan et al., 2002). This effect is partly mediated through an increase in litter heterogeneity, which has been shown to have a positive genetic correlation with the proportion of dead piglets during the suckling period (Damgaard et al., 2003). Selection for a reduced litter

heterogeneity is feasible, as demonstrated by a selection experiment in rabbits (Garreau et al., 2008), and is likely to be associated with a reduced mortality (Knol et al., 2002b; Garreau et al., 2008).

1.3.2.2. Sow longevity

Sow longevity is barely considered in nucleus herds, as optimising breeding designs in pigs leads to short generation intervals on both male and female pathways (De Vries et al., 1989b). The situation is different at the commercial level, as a reduced longevity is associated with a higher culling rate, resulting in an increased number of replacement gilts to purchase, in an increased risk of disease due to the introduction of a larger number of new animals into the herd. It is also associated with a lower sow lifetime productivity and a lower herd average litter size due to a higher proportion of first and second litters, which are lower than adult litter sizes. A reduced sow productivity is thus associated with increased costs, lower returns and, therefore, a decreased farmer's profitability. Sow longevity is defined as the time interval from birth or from the end of fattening to culling. It is often replaced by the length of productive life, i.e. the interval from first pregnancy or first farrowing until culling. It can also be indirectly evaluated from culling rate, replacement rate or the average number of parities at culling.

Several authors have reported unfavourable correlations between production and reproduction traits and longevity. Higher litter sizes have been associated with larger losses of body condition, a higher prevalence of shoulder lesions with, consequently, a reduced welfare and a potentially decreased longevity (Prunier et al., 2010; Ocepek et al., 2016). Relationships between production traits and longevity vary according to studies. A genetic antagonism was reported by e.g., Wongsakajornkit and Imboonta, (2015), while a genetic independence was obtained in other studies Sobczynska et al. (2013). Selection on backfat thickness and growth rate had unfavourable effects on longevity (Tarrés et al., 2006; López-Serrano et al., 1999; Knauer et al., 2010). Selection for backfat thickness influenced longevity through leg weakness syndrome (Rothschild and Christian, 1988). Kadarmideen et al. (2004) supported these results by showing genetic antagonism of productive traits with osteochondrosis (bone abnormalities). However, Kristensen and Sollested, (2004) found no significant association between longevity and average daily gain whereas López-Serrano et al., (2000) showed unfavorable correlation. In the same study, López-Serrano et al. (2000) reported that back fat thickness had unfavorable correlation with longevity. Sow with low feed intake during lactation which were observed in the modern sow have resulted in shorter lifetime (Serenius and Stalder, 2006). Sow which is selected for reproductive traits produced offspring with a low growth rate and poor carcass quality but longer lifetime productivity (Cassady et al., 2004; Serenius and

Stalder, 2006). Different results can be found in the scientific literature regarding the association between longevity and such economically important production traits but the differences may be due to different culling strategies. Decision to cull sow consider several factors such as fertility, disease, feet and leg soundness, housing, behavior and nutrition (Stalder et al., 2004).

1.3.2.3. Sow behaviour

Sow behaviour includes several components, i.e. group behaviour, reaction to humans and reaction towards their progeny during the farrowing and nursing periods. Low to moderate heritability values have been reported for sow behavioural traits (e.g. Gäde et al, 2007; Canario et al., 2013). Selection for high production and reproduction efficiency could have produced undesirable effects on sow behaviour that may affect their welfare and that of their piglets (Rauw et al., 1998; Canario et al., 2013). In particular, selection would increase the sensitivity of animals to environmental stress (Grandin and Deesing, 2014). Canario et al. (2014b) showed that “modern” sows are more reactive to farrowing stress and would then be were less attentive to their piglets, which would increase the risk of piglet crushing. Unfavourable genetic correlations between lean content and sexual behaviour, i.e. oestrus length and intensity of vulvae symptom and ability to show a standing reflex have also been reported by Rydhmer et al. (1994).

1.3.3. Robustness

Robustness is often considered as one of the major traits adversely affected by selection for increased performance (Rauw et al., 1998; Dourmad et al., 2010; Mormède et al., 2011; Phocas et al., 2014). Robustness is a complex trait with somewhat different definitions in the literature. In their review, Sauvant and Martin, (2010) defined it as the dynamic response of a system (which may be an animal) to face a stressor or a perturbation, which can be characterised by the time to respond (or incubation time), its amplitude and the time necessary to come back to the initial condition, called resilience. Animals may adapt to the perturbation by either resisting (rigidity): pigs remain unchanged by the perturbation, distorting (elasticity or flexibility): pigs respond to the perturbation, but come back to the initial condition, or changing (plasticity): pigs change and adapt. Robustness may be related to each of these mechanisms. Knap (2005) defined robustness as “the ability to combine a high production potential with resilience to stressors, allowing for unproblematic expression of a high production potential in a wide variety of environmental conditions”, while Calus et al. (2013) described a robust cow as a cow that is able to maintain homeostasis in a range of production environments. These definitions are linked to rigidity, but also include elasticity and plasticity components. As emphasized by Rauw and Gomez-Raya (2015), sensitivity to macro-

environments can be characterized by the variability across discrete environments or by reaction norms to continuous environmental variations, whereas environmental variance will measure micro-environmental sensitivity.

Selection for high production efficiency has produced animals that are more at risk with respect to major biological functions. One potential reason is an increased competition between biological functions (trade-offs). Resources are more likely to be limited in high performance animal, so that, according to resource allocation theory by Beilharz et al. (1993), they would have increased difficulties to correctly allocate resources between biological functions when they are submitted to environmental perturbations. Changes in cortisol production have also been hypothesised as a potential cause of decreased robustness (Foury et al., 2009; Mormède et al., 2011).

Improving the robustness of livestock species is a major challenge for the future for several reasons. A first major reason is to reduce the use of antibiotics in livestock production because of scientific concern that resistance selected in animals might be transmitted to humans and be detrimental for their health. Transmission may pass through handling of animals or food derived from animals. Additionally, Anadón and Martínez-Larrañaga (1999) showed that residues of antibiotics can be detected in pig and chicken carcasses. Europe has banned growth-promoting antibiotic, even though some have argued that regulation of animal use of antimicrobials should wait scientific certainty about the magnitude of the risk to people (Singer et al., 2003). As a result, there were some diminution of *vancomycin resistance enterococci* (VRE) isolated from human faeces, but an increased morbidity and mortality in pig and poultry (Casewell et al., 2003). More robust animals are thus required to better face microbial risks.

A second reason is climate change, which is expected to have direct and indirect impacts on livestock populations, particularly in Africa. Direct impacts include increased ambient temperature, floods and droughts. Increased temperature is likely to impair productive (growth, meat, milk yields and quality) and reproductive performance, metabolism, health status and immune response (Nardone et al., 2010). Indirect impacts are the result of reduced availability of water and forage, which may have critical effects the availability, variability and stability of food supplies (Thornton et al., 2009). Changes in the environment may also promote the spread of contagious diseases through increased contacts between animals, or increased survival or availability of the agent or its intermediate hosts (Hoffmann, 2010; Nardone et al., 2010; Wheeler and Reynolds, 2012). The potential vulnerability of the livestock industry will depend on its ability to cope with such changes. Enhancing this capacity presents a practical way of coping with climate change.

The third reason is competition between human and livestock food resources, which is likely to result in lower and more variable quality of feed given to animals. The fourth one is the above-mentioned increased environmental sensitivity of animals, which has resulted in their decreasing capability to maintain their production in some environments. The last one is the globalization of pig industry, which leads pig breeders to distribute the same populations throughout the world in a wide range of environment with varying climates, housing facilities, exposure to different pathogens and feed quality. Most nucleus herds are established in temperate countries, and the improved breeding pigs distributed across countries. International breeds of European or North American origin such as Yorkshire, Landrace, Duroc, Piétrain or Berkshire are most widely used populations in developing countries (Huynh et al., 2007). These breeds selected to adapt to temperate climate are supposed to be able to adapt to tropical areas. Breeding organisations should produce robust pigs that maintain their productivity levels across environments.

According to Knap (2009), two complementary options can be used to reach this goal: 1) estimating breeding values for environmental sensitivity of the genetic potential for production performance using reaction norm models (Silva et al., 2014; Herrero-Medrano., 2015), 2) include measurable robustness traits in the breeding goal and the selection index. Functional traits such as fertility, leg weakness, longevity or health traits, as well as behavioural traits related to animal welfare are good candidates for such robustness traits (Rauw and Gomez-Raya, 2015). In the case of no known cause of environmental variation, selection to reduce environmental sensitivity may be used. There is some empirical evidence that genetic variation in residual variance exists between animals (Ibanez-Escriche et al., 2008; Mulder et al., 2009).

It should be pointed out that homogeneity may be important for other reasons. For instance, the homogeneity of birth weight is related to pre-weaning piglet survival (Damgaard et al., 2003; Huby et al., 2003) and pig body weight at slaughter (Ibanez-Escriche et al., 2008). The heterogeneity of slaughter pig weight is associated with reduced selling prices of pigs outside the “normal” weight range (Hennesy, 2005).

2. -Estimation of the effects of selection on sow reproductive performance in French Large White breed from 1977-1998

Until the mid of 1980's, French pig populations have been selected for production traits, i.e. growth rate, feed efficiency and carcass lean content. Selection was based on individual selection indexes. Two different indexes were used: an on-farm index based on age at 100 kg (A100) and average backfat thickness (ABT) was used to select replacement gilts and natural service boars for both nucleus and multiplication herds; an individual index based on average daily gain, feed conversion ratio and ABT was used to evaluate station tested young boars for artificial insemination and some natural service boars. In 1985, a meat quality phenotypic index (MQI) computed as a linear combination of pH, color and water holding capacity was added to the breeding goal (Jacquet et al., 1984). As meat quality measurements could be performed on carcasses only, the individual index of station tested pigs was replaced by a combined index including the performance of the young boar candidate and of two slaughtered sibs. In addition to ADG, FCR and ABT measured on candidates, the index included ADG, FCR, dressing%, carcass lean content and MQI. At the end of the 1980's, "hyperprolific" breeding schemes were developed by selecting sows and boars on the basis of a prolificacy index (Herment et al., 1994). In Large White breed, the hyperprolific scheme benefited from previous work developed at INRA (Legault and Gruand, 1976). In the mid 1990's, litter size was officially included in the breeding goal of French Large White and Landrace breeds and standard selection indexes were replaced by BLUP-animal model of the genetic evaluation method for both production and reproduction traits. Until 2002, total number born was used as the single selection criterion for reproductive traits (Tribout et al., 1998).

As mentioned in chapter 1, genetic trends over 5 (for production traits) or 10 years (reproduction traits) were provided periodically to breeding organizations and to farmers as a by-product of the genetic evaluation process. Genetic trends over longer periods of time have been estimated (see chapter 1), but these genetic trends were in all cases limited to the traits used as selection criteria. The use of frozen semen allows a large number of traits to be measured. Such trends have been estimated after 5, 10 and 20 years of selection for production and quality traits, but the current experiment was the first one to estimate genetic trends for a wider range of traits

including behavioral, male and female reproduction traits as well as trait homogeneity, which will receive a particular attention in this thesis. The effects of selection on reproduction traits and their consequences on progeny survival and growth were investigated in four different parts of the thesis. The first part will analyze the effects of selection on male and female sexual maturity, as well as sow reproductive performance until farrowing. The second part will investigate the effects of selection on sow and piglet performances during the suckling period. In the third part, the effects of selection on the variability of the fattening performance of the progeny and on the phenotypic correlations between traits are investigated. The fourth part investigates the influence of selection on sow macro-environment effects on their offspring performance.

2.1. Experimental Design

Animals

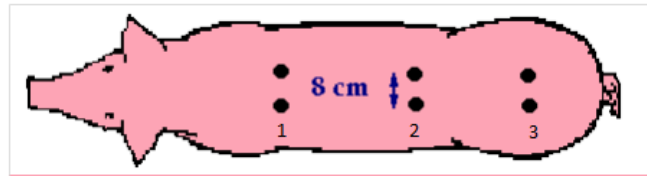
Animals used in this study were raised and slaughtered in accredited slaughterhouses according to the protection of animals rules defined in the French law (Code Rural, articles R214-64 to R214-71 (Legifrance, 2016)). French Large White (**LW**) sows born in 1997 to 1998 were inseminated in the INRA GENESI (Génétique, Expérimentation et Systèmes innovants) experimental unit (Surgères, France) with stored frozen semen from either 17 LW boars born in 1977 (**S77**) or with fresh semen from 23 LW boars born in 1998 (**S98**). During the 1977 through 1998 period of time, the French LW population has been selected for growth rate, feed efficiency, and carcass composition. Additional traits, i.e. meat quality and litter size, were added to the breeding objective in 1985 and 1990, respectively.

Thirty and 33 litters were produced from S77 and S98 boars, respectively. Pigs from these litters were noted as L77 and L98, respectively. After weaning at 4 weeks of age, half of the piglets from each litter and sex were transferred to another INRA experimental herd located near Bourges (Avord 18520). They were raised in pens of 12 animals and pigs were fed ad libitum with a standard pelleted diet containing 3200-3300 kcal DE/kg from 10 to 22 week of age (**Le Magneraud**) or 26 weeks of age (**Bourges**).

Male sexual development was characterized by measuring the total width of testes at 14, 18, 22, and 26 wk of age (**TW_x**, in which $x = 14, 18, 22, \text{ or } 26$) and the length of the bulbourethral gland at 22 and 26 wk of age (**BUL22** and **BUL26**, respectively) measured by echotomography as described by Sellier et al. (2000). Fifteen L77 and 15 L98 unrelated males were randomly chosen and kept for reproduction. All remaining males were slaughtered at 26 wk of age and measured for testes weight (**TWESL**), testes length (**TLSL**), testes width (**TWISL**), bulbourethral gland length (**BULSL**), bulbourethral gland weight (**BUWSL**), and epididymis weight (**EPWSL**).

Female sexual development was checked from 150 to 260 d of age: 1) through a daily detection of estrus by introducing a sexually mature boar in each pen and 2) through the detection of ovulation using blood samples collected every 10 d and assayed for plasma progesterone as described by Prunier and Meunier-Salaun (1989). Ovulation was considered as having occurred when progesterone concentration was higher than 5 ng/mL. Age at puberty (**AGEPUB**) was then estimated by combining progesterone and estrus records as described by Bidanel et al. (2008). Ten to 13 d after

reaching puberty, gilts were weighed [BWPUB]) and ovulation rate (ORP) was estimated by counting corpora lutea on each ovary (number of corpora lutea on the left and the right ovary [ORPL and ORPR, respectively]) through laparoscopy.



Picture 2.1. Backfat Thickness Measurement Points

In both herds, pigs were individually weighed at 10 and 22 wk of age (IB10W and IBW22W, respectively) and measured for backfat thickness at 22 wk of age at 6 locations (on each side of the spine, 4 cm from the mid-dorsal line at the shoulder, the last rib and the hip joint, respectively) using a real-time ultrasound Aloka SSD-500 device (Ecotro Aloka, Tokyo, Japan).

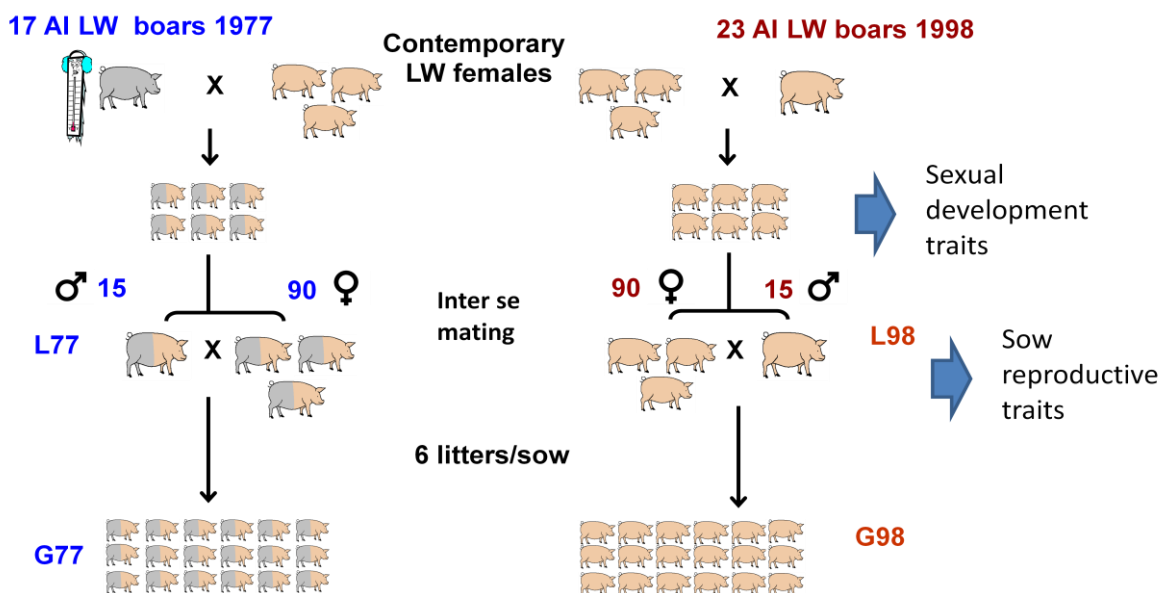


Figure 2.2. Experimental design for sexual developmental and sow reproduction analysis;

G77, G98 = experimental groups of piglets produced by L77 and L98 sows, respectively; L77 = experimental group produced by inseminating Large White sows with either stored, frozen semen from 17 Large White boars born in 1977; L98 = experimental group produced by inseminating Large White sows with semen from 23 Large White boars born in 1998.

A total of 15 males and 90 females from L77 and L98 respectively (2 to 3 pigs per litter) were then randomly chosen. Females were then kept in collective pens and were fed 2.5 to 3 kg of a commercial sow diet during the whole gestation period. They were managed under a batch farrowing system, with 3-wk intervals between successive batches. Gilts were submitted to a synchronization treatment with a progestagen to integrate farrowing batches. When estrus was detected, females were inseminated twice within a 12-h interval with semen from unrelated boars from the same experimental group. Females that were not pregnant after the first mating were

allowed to rebreed 3 wk later but were culled if this second mating was unsuccessful. Three wk after fertilization, ovulation rate at fertilization (**ORF** = ovulation rate of gestating sows) was estimated by measuring the number of corpora lutea on the left and right ovaries (ovulation rate at fertilization on the left and the right ovary [**ORFL** and **ORFR**, respectively]) through laparoscopy.

They were transferred to the farrowing unit 1 wk before the expected day of farrowing. They were placed in individual farrowing crates with slatted floor until weaning. Farrowing was induced with prostaglandin on the 113th day of gestation. The day of farrowing, the number of stillbirths (**SB**), the number of mummified piglets, and the number born alive (**NBA**) were recorded for each litter. All piglets born were individually weighed within 24 h after farrowing. All piglets from each farrowing batch were weaned on the same day at 4 wk of age. Sows were inseminated again on their first estrus after weaning.

When possible (i.e. when L77 and L98 sows farrowed on the same day or at a one-day interval), piglets were crossfostered at about one day of age in order to have a 2 x 2 factorial design with mixed G77 /G98 litters nursed by either L77 or L98 sows so as to disentangle sow and litter effects on piglet growth. During lactation, sows were given a diet containing a minimum of 13.8 MJ DE, 160g CP and 7.6 g total lysine per kg. They were given an increasing quantity of feed from day one after farrowing to day 5. They were then fed semi-ad libitum on the basis of their feed consumption in the previous day. Sow feed intake was recorded volumetrically from farrowing to weaning at 4 wk of age in GENESI experimental unit. Sows were weighed again at weaning.

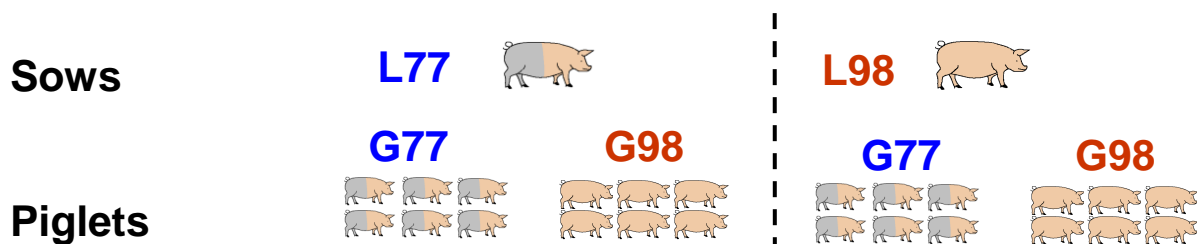


Figure 2.3. Experimental design for sow and piglets analysis during lactation

G77, G98 = experimental groups of piglets produced by L77 and L98 sows, respectively; L77 = experimental group produced by inseminating Large White sows with either stored, frozen semen from 17 Large White boars born in 1977; L98 = experimental group produced by inseminating Large White sows with semen from 23 Large White boars born in 1998.

Colostrum samples were collected at the birth of the first and the last piglet from each litter and 24 hours after farrowing. A milk sample was then collected 14 d after farrowing. All samples were collected after an oxytocin injection. Samples were analyzed to determine their dry matter (**DM**), crude protein (**PR**), lactose (**LACTO**) and fat (**FAT**) content. Crude protein content was calculated by multiplying the N content of colostrum and milk by a conversion factor of 6.25.

When piglets died, the date and, when known, the cause of death were recorded. Identified causes of death were stillbirth, crushing, general weakness and cannibalism. Piglets born in these litters are referred to as **G77** (offspring of L77) and **G98** (offspring of L98) experimental groups. The 2733 G77 and 3432 G98 piglets born were individually weighed at birth (**IBW**) within 24 hours after farrowing, i.e. before crossfostering. Alive piglets were then weighed again at 21 d of age (**IW21d**) and at weaning at 4 wk of age (**IWW**). No creep feed was distributed to piglets before 21 d of age in order to accurately estimate sow milk production. After 21 d of age, they were given access to creep feed formulated to contain a minimum of 14.7 MJ DE, 174g CP, 14.7 g Lysine and 5.8 g methionine.

A total of 1697 G77 and 1920 G98 pigs were then performance tested in Le Magneraud and Bourges experimental herds between 10 wk of age and 105 kg live weight as described by Tribout et al. (2010). Pigs were raised in pens of 12 animals, where they were given ad libitum access to water and to a standard pelleted diet formulated to contain 3.200 DE/kg and 17% CP from 10 weeks of age until slaughter. Pigs were weighed individually at 10 wk (**IW10W**) and at 20 wk (**IW20W**) of age, and then the day before slaughter at 23 wk of age on average (**IWSL**). Most pigs were also measured ultrasonically for backfat thickness at 20 wk of age (**ABFT20W**) at 6 locations (on each side of the spine, 4 cm from the mid-dorsal line at the shoulder, the last rib and the hip joint, respectively) using the above-mentioned ultrasound Aloka SSD-500 device.

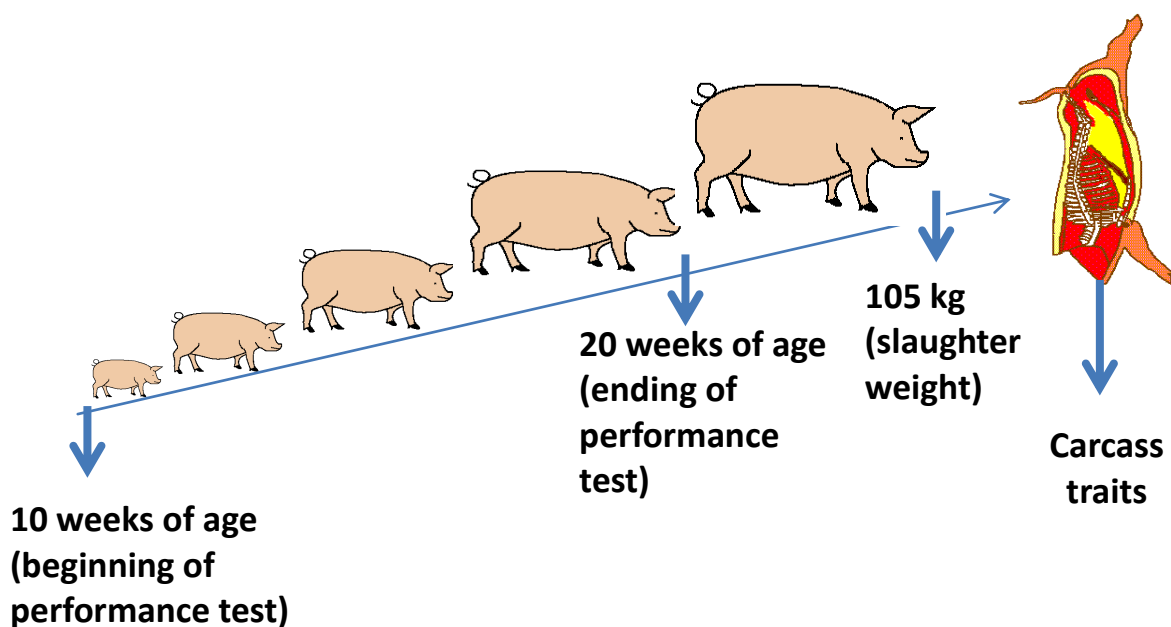


Figure 2.4. Performance tested pigs, slaughter pigs and carcass traits; performance test was performed from 10 to 20 wk of age; slaughter took place at 105kg live weight in average;

When reaching 105 kg live weight (**IWSL**), pigs were sent to commercial slaughterhouses. Pigs were individually weighed at 10 and 20 wk of age and also the day before slaughter (23rd wk of age, on average, varying from 135 to 199 d of age in both the G77 and G98 groups). At the end of the test period, 2 samples of 120 animals fattened in the *Bourges*, balanced for experimental group and sex, were slaughtered in the INRA experimental slaughterhouses of Jouy-en-Josas and Saint-Gilles, respectively. The remaining pigs were slaughtered in different commercial slaughterhouses [i.e., Montfort-sur-Meu (Cooperl-Hunaudaye, Montfort-sur-Meu, France), Celles-sur-Belle (Socopa, Celles sur Belle, France), and Orléans Viande (Fleury les Aubrais, France) for pigs from the *Le Rheu*, *GENESI*, and *Bourges* units, respectively]. The same measurement protocol was applied in the different slaughterhouses.

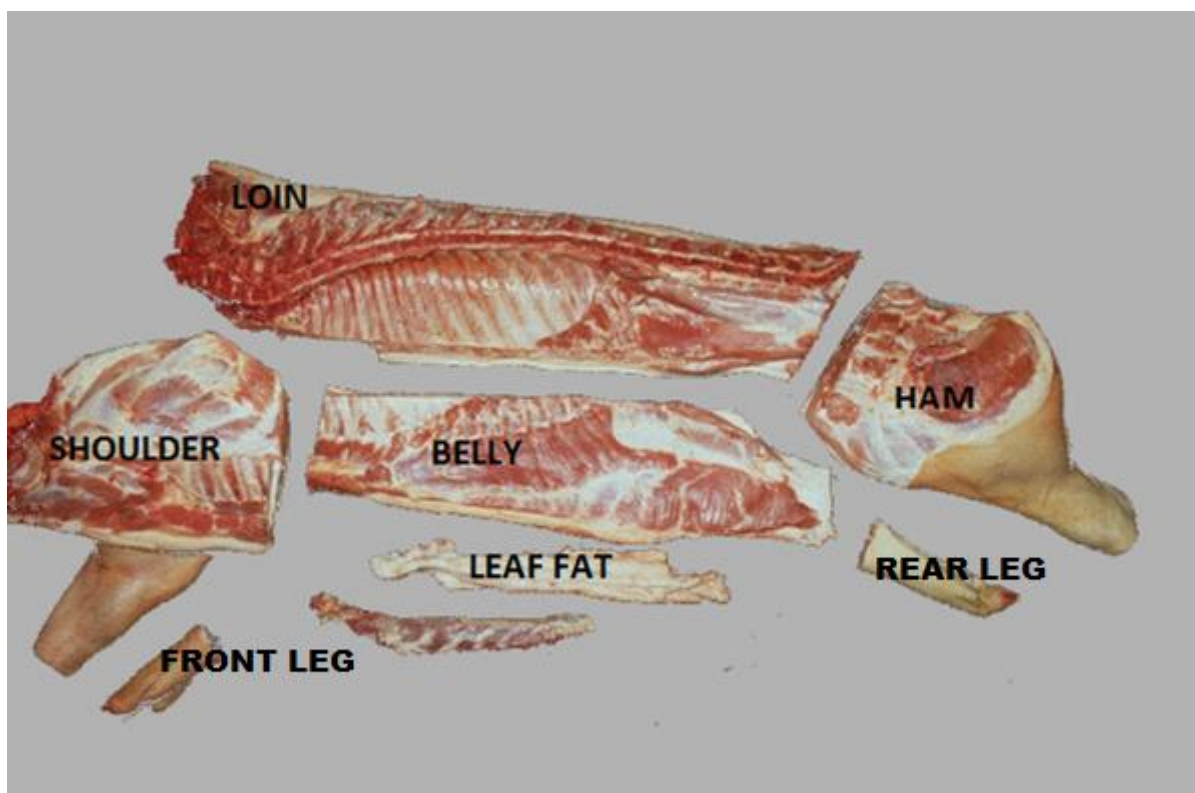


Figure 2.5. Carcass primal cuts; the same measurement protocol was applied in the different slaughterhouses

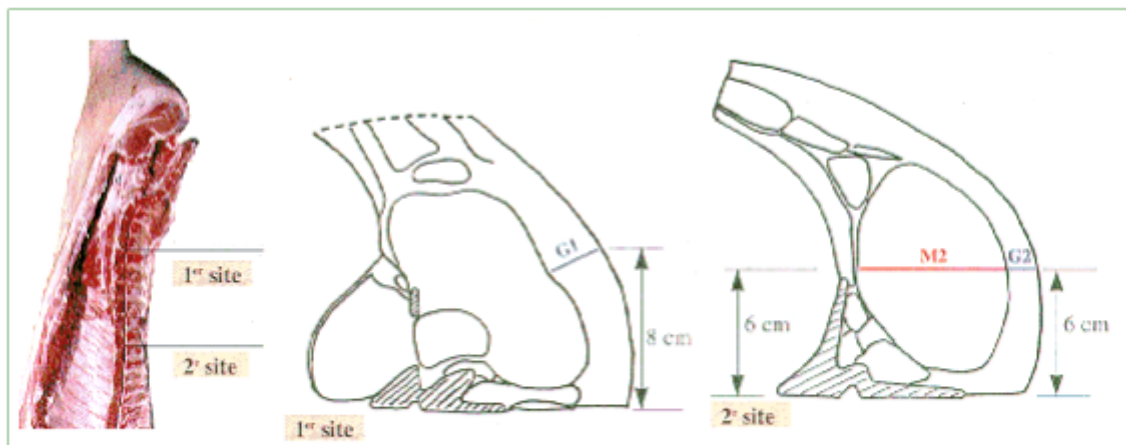
Traits and Statistical Analyses

All sexual development traits, i.e. TWI14, TWI18, TWI22, TWI26, BUL22, BUL26, TWESL, TLSL, TWISL, BULSL, BUWSL, and EPWSL for males and AGE PUB, BW PUB, ORP, ORPL, and ORPR for gilts, were analyzed using mixed linear models including herd, fattening batch within herd, and experimental group as fixed effects, birth litter as a random effect and either BW (for all male traits) or age at measurement (for ORP, ORPL, and ORPR) as covariates, using SAS MIXED procedure (SAS Inst.

Inc., Cary, NC). Contrary to Tribout et al. (2010), genetic relationships within groups were ignored, as preliminary analyses showed that results were very similar with or without considering these relationships.

Female reproduction traits included NBA, SB, the total number of piglets born per litter (total number born **[TNB]** = NBA + SB), and litter weight at birth (**LWB**), computed as the sum of individual piglet weights at birth, as well as components of litter size, that is, ORFL, ORFR, and ORF and prenatal survival rate (**PSURV**), defined as the ratio $PSURV = TNB1/ORF$, with **TNB1** corresponding to TNB in the subset of litters with ovulation rate data. Additional traits, i.e. interval from weaning to first estrus, farrowing interval, and length of productive life, computed as the period of time between first successful mating until last weaning, were also analyzed. These reproduction traits were analyzed using a mixed linear model including herd, farrowing batch within herd, experimental group, and parity as fixed effects and sow as a random effect. Litter weight at birth was analyzed with and without adjustment for TNB.

figure 2.6. Additional measurements used for carcass grading using CGM probe



G1: BFT between the third and fourth lumbar vertebrae

G2: BFT between the third and fourth last rib

M2: loin eye depth between the third and fourth last rib

During lactation, sow traits analyzed included number of piglets nursed by each sow at d 1 after cross-fostering (**NNd1**), at d 21 (**NNd21**) and at weaning (**NW**), litter survival rate, computed as $\%SURV = 100 \times (NW : NNd1)$, litter weight, computed as the sum of individual piglet weights, at d 1 (**LWd1**), at d 21 (**LWd21**) and at weaning (**LWW**), sow weight before farrowing (**SWF**) and at weaning (**SWW**), sow total weight loss (**STWL**) from farrowing to weaning, computed as $STWL = SWF - SWW$, sow net weight loss (**SNWL**) from farrowing to weaning, computed as : $SNWL = STWL - 0.3 - 1.329 * LWB$, where **LWB** = litter weight at birth (Dourmad et al., 1997), sow daily feed intake from farrowing to weaning (**DFI**), milk production (**MILKP**) estimated as $MILKP = [(4 * ADG21 - 39) * NNd21]$, where **ADG21** = piglets average daily gain from birth to 21 d of age – see below). This equation is based on

the milk dry matter (DM) prediction equation of Noblet and Etienne (1989) and a milk DM content of 18%, as suggested by Etienne et al. (2000). Analyses were performed using mixed linear models including herd, farrowing batch within herd, experimental group as fixed effects, sow as a random effect. **LWd1**, **LWd21** and **LWW** were analyzed with and without adjustment for litter size, i.e. **NNd1**, **NNd21** and **NW**, respectively. Analyses were performed using SAS MIXED procedure. Interactions between fixed effects were tested in preliminary analyses, but none of them reached significance ($P < 0.10$) or had any noticeable effects on experimental group effects. As in Silalahi et al. (2016), the heterogeneity of variances across experimental groups (L77 vs L98) was tested in preliminary analyses using a likelihood ratio test.

Piglet traits analyzed included: 1) mortality traits, i.e. stillbirth (**SB**), mortality on day one (**MORTd1**), i.e. before cross-fostering, and from day 2 to weaning (**MORTd2W**), as well as potential differences in major causes of mortality, i.e. crushing (**MORT_CR**) and general weakness due to chilling and starvation (**MORT_GW**); 2) traits related to piglet growth during the nursing period, i.e. **IBW**, **IW21d** and **IWW**, as well as average daily gain from birth to 21d of age (**ADG21d**) and from birth to weaning (**ADGBW**). Mortality traits were analyzed using generalized mixed models (GLMM) using the GLIMMIX procedure of SAS (SAS Inst., Cary, NC), whereas the MIXED procedure of SAS was used for growth traits. In both cases, the models used included experimental group, sex, herd, batch within herd and parity of the dam as fixed effects, birth or nursing litter as a random effect and, in additional analyses, litter size and IWB as covariates. Two levels (L77 and L98) were considered for the experimental group effect for traits measured before cross-fostering. After cross-fostering, six levels were considered in first analyses: G77 piglets nursed by L77 sows in litters with only G77 piglets (unmixed litters – level 1), in mixed G77/G98 litters (level 2) or nursed by L98 females (level 3); G98 piglets nursed by L98 dams in unmixed (level 4) or mixed (level 5) litters, or nursed by L77 sows (level 6). These six levels were reduced to four levels when piglet nursed in mixed vs unmixed litters of the same sow group has similar performances.

Growth traits analyzed were individual weights at 10 and 20 wk of age and before slaughter (**IW10W**, **IW20W**, **IWSL**, respectively), as well as average daily gain (ADG) from weaning to 10 wk of age (**ADG10W**) and from 10 wk of age to 20 wk of age (**ADG20W**). Carcass traits analyzed included average backfat thickness at 20 wk of age (**ABT20W**), computed as the mean of the 6 ultrasonic backfat measurements, carcass weight (**CWT**), carcass length (**CL**) and estimated carcass lean content, computed from CGM probe measurements (Sydel, Lorient, France) using the equations of Daumas et al. (1998), as well as carcass cut weights, i.e. ham (**HAMWT**), loin (**LOINWT**), shoulder (**SHWT**), Backfat (**BFWT**) and belly (**BELWT**) weights.

The effects of sow macro-environmental effects were investigated by adding each of them as a covariate in the analyses of growth and carcass traits. Effects investigated were gestation length (**GL**), computed as the difference between the date of farrowing and the date of first insemination, total number born (**TNB**), number born alive (**NBA**), litter weight at birth (**LWB**), computed as the sum of individual piglet weights from the same litter at birth, sow weight before farrowing (**SWF**) and at weaning (**SWW**), sow net weight loss (**SNWL**) from farrowing to weaning, computed from sow total weight loss (**STWL = SWF – SWW**) and (**SNWL = STWL - 0.3 - 1.329 * LWB** - Dourmad et al., 1997). Young sow traits, i.e. age (**AGEPUB**) and body weight (**BWPUB**) at puberty as well as age at first farrowing (**AGEF**) were also considered. The different macro-environmental effects were then added to the base model (1 at a time) as covariates, either globally or within-experimental group. Potential non-linearities between the covariate(s) and the trait analyzed were tested in preliminary analyses by adding a quadratic term to the model and by analyzing residuals.

Interactions between fixed factors, in particular between experimental group and herd or parity, were tested in preliminary analyses. They were removed from final analyses when they were non-significant ($P > 0.10$) and had a limited effect on experimental group effects. The heterogeneity of variance across experimental groups was also tested in preliminary analyses using a likelihood ratio test. When variances were significantly different, the final analyses were performed using a model with different residual variances in both genetic groups using the REPEATED statement of the SAS MIXED procedure. Residual values were then used to compute: 1) within experimental group and within litter standard deviations (WLSD), 2) global and within experimental group residual correlations with the residual value of birth weight, global and within experimental group correlations between WLSD for each trait and WLSD for birth weight.

Estimate genetic trend (ΔG_a)

The genetic trend (ΔG) and its SE for each trait was computed as (Smith, 1977):

$$\Delta G = 2 \times (\mu_{L98} - \mu_{L77}) \text{ and}$$

$$SE(\Delta G) = 2 \times SE_{L98-L77},$$

in which μ_{L98} and μ_{L77} are estimates of experimental group effects and $SE_{L98-L77}$ is the SE of the contrast between L98 and L77.

Power of design (Tribout et al., 2010)

The power of the actual design (i.e., the probability of detecting a trend if it exists) can be computed as the power of a 2-sided test (i.e., hypothesis 1, $\mu_{98} \neq \mu_{77}$ vs null hypothesis, $\mu_{98} = \mu_{77}$).

$$Pr[T > (\alpha)] = Pr \left[U < \frac{\mu_{77} - \mu_{98}}{\sigma} - z(1 - \alpha/2) \right] + Pr \left[U > \frac{\mu_{77} - \mu_{98}}{\sigma} + z(1 - \frac{\alpha}{2}) \right]$$

Where α is the significant level of test,

$T_e(\alpha)$ is the α -level critical value,

$$U = (T - \mu_{98} - \mu_{77})/\rho \sim N(0,1)$$

and

$$z(1-\alpha/2)$$

is the $(1-\alpha/2)$ -level critical value of U.

Ignoring covariances between experimental groups attributable to female founders, the variance α^2 is the sum of the sampling variance of the mean of each experimental group, calculated as (Smith 1977);

$$V = [1 + (n - 1)t_1 + n(d - 1)t_2]/nds$$

s is the number of sires, d is the number of dams per sire, n is the number of offspring per dam, and t_1 and t_2 are, respectively, the phenotypic correlations between full-sibs ($t_1 = h^2/2 + c^2$, where h^2 is the heritability of the trait and c^2 is the proportion of phenotypic variance from birth litter environmental origin), and half sibs ($t_2 = h^2/4$) (Falconer and Mackay, 1996).

Four cases were considered, according to the size of the G77 and G98 samples and their familial structure in the present design:

- A) $nds = 1,000$ pigs, $ds = 75$ dams, and $s = 18$ boars;
- B) $nds = 500$ animals, $ds = 75$ dams, and $s = 18$ boars;
- C) $nds = 180$ animals, $ds = 56$ dams, and $s = 18$ boars;
- D) $nds = 120$ animals, $ds = 48$ dams, and $s = 17$ boars.

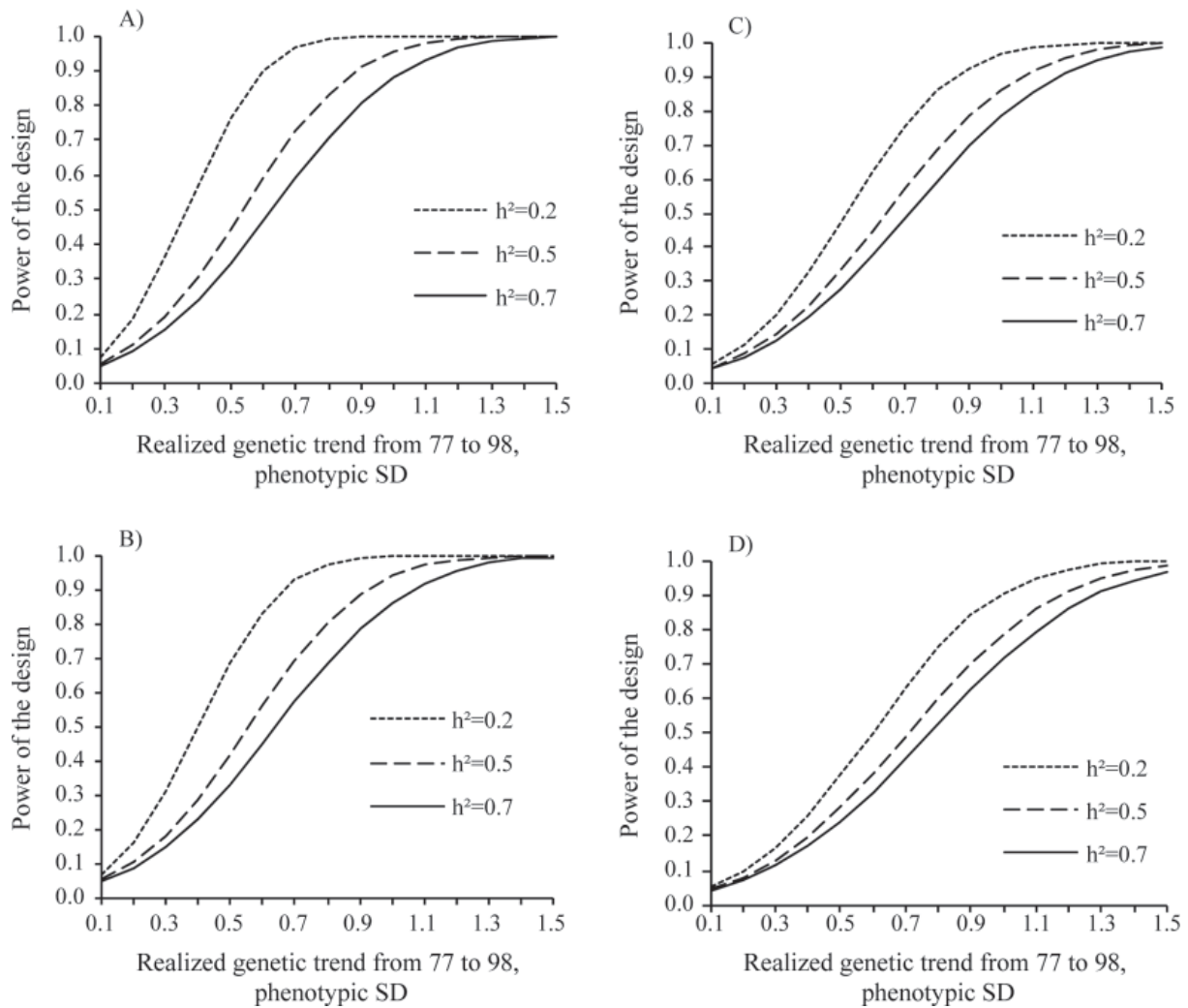


Figure 2.7. Power of the design for different sample sizes and heritability (h^2) values, as a function of the realized genetic trend from 1977 to 1998 (in phenotypic SD units), assuming a 5% type I error. A) Offspring ($n = 1,000$) from 18 boars and 75 dams measured in each experimental group. B) Offspring ($n = 500$) from 18 boars and 75 dams measured in each experimental group. C) Offspring ($n = 180$) from 18 boars and 56 dams measured in each experimental group. D) Offspring ($n = 120$) from 17 boars and 48 dams measured in each experimental group (from Tribout et al., 2010)

Three heritabilities ($h^2 = 0.2, 0.5, \text{ and } 0.7$), corresponding to the range of heritability values for the traits investigated, were considered for each of the 4 cases. According to Tribout et al. (2010), a sensitivity analysis on performance test pigs by increasing and decreasing the heritabilities used in PEST by 30% gave results that remained unchanged. The lack of difference between results from analyses with and without considering relationship between pigs has led us to perform analysis without pedigree information for all the analyses.

2.2. Effects of 21 years of selection on sow reproductive performance in French Large White population

Both male and female sexual development and reproductive performance were investigated in this experiment. Results have been published in Journal of Animal Science with the title “**Estimation the effect of selection on French large white reproductive performance using frozen semen**”.

A stronger emphasis was put on female reproduction, with larger numbers of animals measured, because of its much larger economic impact. The effects of selection on the development of sexual maturity in both sexes were analyzed in this first study, but only female reproduction traits will be focused. Male reproductive performances have been investigated through semen quality (sperm concentration, viability and motility) of first generation young boars, but could not be repeated on second generation males. No differences of semen quality were detected between L77 and L98 experimental groups. The results of semen quality are not presented here because of the too small number of animals measured and, consequently, the lack of power of the experiment. A full assessment of male reproductive efficiency would have required to collect data on fertility rates. It was not considered, as there is little or no indication in the literature of adverse effects of selection on boar fertility, and because it would have required thousands of records to get the necessary power.

Puberty is a major event of sexual maturation. It is defined in gilts by the occurrence of the first ovulation. It is usually assessed by first estrus, a simple, though rather tedious, measurement. It is considered as rather accurate, but it can be biased by either estrus behavior without ovulation or ovulation without visible estrus behavior. Estrus behavior measurement was hence complemented by progesterone measurements every ten days. The combination of both measurements eliminates the risk of false or silent ovulation. Puberty in boars is indicated by age at the first appearance of spermatozoa in *tubulus seminifer*. It is much more difficult to measure than in females, so that it is often replaced by indirect measurements such as testosterone levels or the development of sexual organs. This last option was chosen in the current study by measuring testes, *bulbourethral* glands and *epididymis* weights. Results showed that L98 boars had a larger epididymis weight than L77. It tends to indicate that “modern” boars were able to store a larger number of spermatozoa (Okwun et al., 1996). Testis length was also longer in G98 boars, but no difference was observed for testis width or *bulbo-urethral* gland weight.

Rather simple reproductive measurements were taken in females. The only exception is the number of corpora lutea, which is measured by laparoscopy, with a general anesthesia and some (very simple) surgery. Conversely, no genital tract measurement, such as ovary or uterus size was performed. It would have been useful to provide data on uterine capacity to supply and on the space and nutrients available for embryos/fetuses. Conception and pregnancy rates are also useful indicators of reproduction performance. In this study, 90 gilts for each genetic group were chosen, and then mated with the boar from the same genetic group. The conception rate was 82% for G77 and for 98% for G98.

Though prolificacy was selected only from the end of the 1980's, a rather important increase in litter size and litter weight was observed. It illustrates the fact that, in spite of its low heritability, litter size can very efficiently be improved by selection in large populations by applying high selection intensities, as first demonstrated by the French "hyperprolific" Large White line (Legault and Gruand, 1976; Bidanel et al., 1994). This gain has been accompanied by a correlative increase in the numbers of piglets born alive, but at the expense of an increase in the number of stillbirths. Even if it may be economically interesting, this trend is not desired by farmers, but also more globally by the society for obvious welfare considerations. Potential reasons for the increased number of stillbirths has been discussed in chapter 1. Changing the selection criterion from total number born to number born alive since 2002 has allowed the negative trend on stillbirths to be stopped. Yet, this strategy has not allowed to reduce stillbirths to a large extent. Including a specific criterion, i.e. the proportion or the probability of stillbirth would probably be necessary to go further in this direction.

Another rather important result from this study is the increased residual variability of litter size and weight. This increased variability indicates a higher sensitivity to the environment, which might be interpreted as a reduced robustness of L98 sows. This increased variability can partly be explained by a scale effect. Yet, this effect is limited, as the difference between groups expressed in coefficient of variation units is close to significance. An additional step would have been to know whether this increased variability is due to a lower permanent environmental effect, as tested for example by Sell-Kubiak et al. (2012; 2013) but the size of the experiment was by far too small to allow this hypothesis to be tested.

Finally, the experiment showed a rather strong decrease of sow longevity. This result is not in line with observed trends for sow longevity at the commercial level, which tend to increase (Dourmad et al., 2010). These divergent trends are not necessarily in contradiction. Longevity is not a major objective in purebred lines because short generation intervals are required to optimize genetic trends, a longevity may have deteriorated due to increasing inbreeding levels (Maignel et al., 1998).

These potential unfavorable effects of inbreeding do not exist in crossbred sows at the commercial level. Moreover, farmers may have adapted their management practices to keep their females longer because of the increasing economic interest of a long productive life. The reasons for the decreased longevity of L98 sows could not be thoroughly investigated. As sow culling rules were the same in the two groups of sows, it may result from a decreased conception rate, but also from other reasons such as a decreased leg quality.

Article 1 (published)

Estimation the effect of selection on French large white reproductive performance using frozen semen ¹

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¹The financial support of the “Innovative actions” from the French Ministry of Agriculture is gratefully acknowledged. The authors thank the staff of INRA Bourges and GENESI experimental herds and of the laboratories implied in this experiment; special thanks are given to Francis Bussièrès for collecting, conditioning and taking care of boar frozen semen for more than 20 yrs.

²PS gratefully acknowledges the Directorate General of Human Resource for Science, Technology and Higher Education, Indonesia, Agreenium and INRA Animal Genetics Division for the financial support of the PhD thesis.

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ABSTRACT: Genetic trends for male and female sexual development and components of litter size and weight at birth (LB) as well as traits related to sow lifetime productivity were estimated in a French Large White (LW) pig population using frozen semen. Two experimental groups (EXP = L77 and L98) were produced by inseminating LW sows with either stored frozen semen from 17 LW boars born in 1977 (EXP = L77) or with semen from 23 LW boars born in 1998 (EXP = L98). In each group, about 100 males were measured for testicular development and bulbo-urethral gland development, and 90 gilts were checked for puberty, among which about 50 gilts were measured for their first ovulation rate at puberty (ORP). The females were then mated to 15 randomly chosen males for each group for 6 successive parities and measured for total number born (TNB), number born alive (NBA), litter weight at birth (LWB), and interval from weaning to first estrus as well as ovulation rate at fertilization (ORF = ovulation rate of gestating sows) on a subset of litters. The data were analyzed using mixed linear models including the fixed effects of EXP, of finishing (sexual development traits) or farrowing group, and parity (LB traits); the random effects of birth litter (sexual development

traits) or sow (LB traits); and, when relevant, age or BW as covariates. The homogeneity of residual variances across EXP was also tested. For each trait, the genetic trend was estimated as twice the difference between L98 and L77. Limited differences were observed for sexual development traits, except for ORF, which increased by $0.17 \pm 0.06/\text{yr}$. The residual SD of NBA (2.7 vs. 2.0; $P = 0.004$) and LWB (3.1 vs. 2.5; $P = 0.03$) were larger in L98 sows than in L77 sows. Positive trends were observed for all litter traits (0.22 ± 0.07 ova, 0.12 ± 0.04 piglet, 0.09 ± 0.04 piglet, and 0.23 ± 0.06 kg/yr for ORF, TNB, NBA, and LWB, respectively) but at the expense of a degradation of prenatal and farrowing survival. A negative trend was also observed for length of productive life (-8.9 ± 3.9 d/ yr). These results suggest that gains in productivity were associated with a loss of robustness.

Key words: frozen semen, genetic trend, reproduction, robustness, swine

Running head: genetic trend estimation using frozen semen

Published in; J. Anim. Sci. 2016.94:1–8

Résumé ; Les progrès génétiques pour la précocité sexuelle mâle et femelle et les composantes de la taille et du poids des porcelets à la naissance, ainsi que les caractères liés à la durée de vie productive des truies ont été estimés dans une population porcine large white française en utilisant de la semence congelée. Deux groupes expérimentaux (EXP = L77 et L98) ont été produits par l'insémination de truies LW contemporaines, soit avec la semence congelée de 17 verrats nés en 1977 (EXP = L77), soit avec la semence fraîche de 23 verrats nés en 1998 (EXP = L98). Dans chaque groupe, une centaine de mâles ont été mesurés pour le développement des testicules, de la glande bulbo-urétrale et 90 femelles ont fait l'objet d'un contrôle de puberté, parmi lesquelles environ 50 femelles ont été mesurées pour leur premier taux d'ovulation à la puberté. Les femelles ont ensuite été accouplées à 15 mâles choisis au hasard dans chaque groupe pendant 6 portées successives et mesurées pour le nombre de porcelets nés totaux (TNB) et nés vivants (NBA), le poids de la portée à la naissance (LWB) et l'intervalle entre le sevrage et le premier œstrus, ainsi que pour le taux d'ovulation à la fécondation (ORF = taux d'ovulation des truies en gestation) sur un sous-ensemble de portées. Les données ont été analysées en utilisant des modèles linéaires mixtes incluant les effets fixes d'EXP, de la bande d'engraissement (caractères de précocité sexuelle) ou de la bande de mise bas et du rang de portée (caractères de portée), Les effets aléatoires de la portée de la naissance (caractères de précocité sexuelle) ou de l'environnement permanent de la truie (caractères de portée), et, lorsque c'était approprié, l'âge ou le poids en covariables. L'homogénéité des variances résiduelles entre EXP a également été testée. Pour chaque caractère, le progrès génétique a été estimé comme deux fois la différence de performances entre L98 et L77. Des différences limitées ont

été observées pour les caractères de précocité sexuelle, sauf pour ORF, qui a augmenté de $0,17 \pm 0,06$ / an. L'écart type résiduel de NBA (2,7 vs 2,0 ; $P = 0,004$) et LWB (3,1 vs 2,5 ; $P = 0,03$) était plus élevé chez les truies L98 que chez les truies L77. Des évolutions positives ont été observées pour tous les caractères de la portée ($0,22 \pm 0,07$ corps jaunes ; $0,12 \pm 0,04$ porcelet ; $0,09 \pm 0,04$ porcelet et $0,23 \pm 0,06$ kg / an pour ORF, TNB, NBA et LWB, respectivement), mais au prix d'une dégradation de la survie pendant la gestation et à la mise bas. Une évolution négative a également été observée pour la durée de vie productive ($-8,9 \pm 3,9$ d / an). Ces résultats suggèrent que les gains de productivité ont été associés à une perte de robustesse.

Mots clés : semence congelée, progrès génétique, reproduction, robustesse, porc

INTRODUCTION

Major pig populations have been intensively selected over the last decades, leading to considerable improvements in production and reproduction traits (Guéry et al., 2009; Tribout et al., 2010). Genetic trends can accurately be estimated from standard BLUP genetic evaluation systems, provided that traits are routinely measured and that the selection process is adequately accounted for (Im et al., 1989). Yet selection affects a much larger number of traits correlated with the selection criteria in a favorable, but also sometimes detrimental, way. Indeed, animals selected for high production efficiency may be more sensitive to behavioral, physiological, or immunological problems, that is, less robust (Rauw et al., 1998; Phocas et al., 2014; Rauw and Gomez-Raya, 2015). These adverse effects of selection are often difficult to reveal, as corresponding traits are not routinely recorded in breeding programs.

As suggested by Smith (1977), the use of stored frozen semen has been shown to be an elegant method to estimate genetic trends for a large number of (usually not recorded) traits. Its principle is to use the frozen material to produce animals that are representative of the population at the beginning of the selection process and compare them with a representative population sample after selection. Such an approach has been successfully used, for example, in rabbits (García and Baselga, 2002; Laborda et al., 2012). In pigs, a stock of frozen semen of French Large White boars born in 1977 and collected at the end of the 1970s was used 2 decades later to estimate genetic trends for a large number of traits. Results for growth and carcass traits, sow behavior, and piglet composition at birth were reported by Canario et al. (2007b), Tribout et al. (2010), and Canario et al. (2014b). The aim of this paper was to estimate the effects of selection on male sexual development and sow reproduction traits including sexual maturity and components of litter size at birth as well as

traits related to sow robustness: longevity, rebreeding success, and homogeneity of litter size along the sow reproductive career (Hermesch et al., 2015).

MATERIALS AND METHODS

Animals

Animals used in this study were raised and slaughtered in accredited slaughterhouses according to the protection of animals rules defined in the French law (Code Rural, articles R214-64 to R214-71; in the French law (Legifrance, 2016). French Large White (**LW**) sows born in 1997 to 1998 were inseminated in the INRA Génétique, Expérimentation et Systèmes innovants (GENESI) experimental unit (Surgères, France) with stored frozen semen from either 17 LW boars born in 1977 (**G77**) or with fresh semen from 23 LW boars born in 1998 (**G98**). During the 1977 through 1998 period of time, the French LW population has been selected for growth rate, feed efficiency, and carcass composition. Additional traits, that is, meat quality and litter size, were added to the breeding objective in 1985 and 1990, respectively (see Tribout et al. [2010] for additional details).

Thirty and 33 litters were produced from G77 and G98, respectively. Pigs from this second generation will be noted as **L77** and **L98**. After weaning, half of piglets from each litter and sex were transferred to another INRA experimental herd located near Bourges (Avord, France). They were raised in pens of 12 animals and fed ad libitum using a standard pelleted diet formulated to contain 3,200 kcal of DE/kg and 17% CP from 10 to 22 wk of age. Additional details on the experimental design can be found in Tribout et al. (2010).

Male sexual development was characterized by measuring the total width of testes at 14, 18, 22, and 26 wk of age (**TW_{ix}**, in which $x = 14, 18, 22, \text{ or } 26$) and the length of the bulbourethral gland at 22 and 26 wk of age (**BUL22** and **BUL26**, respectively) measured by echotomography as described by Sellier et al. (2000). Fifteen L77 and 15 L98 unrelated males were randomly chosen and kept for reproduction. All remaining males were slaughtered at 26 wk of age and measured for testes weight at slaughter (**TWESL**), testes length at slaughter (**TL_{SL}**), testes width at slaughter (**TW_{ISL}**), bulbourethral gland length (**BUL_{SL}**), bulbourethral gland weight (**BUW_{SL}**), and epididymis weight (**EPW_{SL}**).

Female sexual development was checked from 150 to 260 d of age: 1) through a daily detection of estrus by introducing a sexually mature boar in each pen and 2) through the detection of ovulation using blood samples collected every 10 d and assayed for plasma progesterone as described by Prunier and Meunier-Salaun (1989). Ovulation was considered as having occurred when

progesterone concentration was higher than 5 ng/mL. Age at puberty (**AGEPUB**) was then estimated by combining progesterone and estrus records as described by Bidanel et al. (2008). Ten to 13 d after reaching puberty, gilts were weighed (BW at puberty [**BWPUB**]) and ovulation rate at puberty (**ORP**) was estimated by counting corpora lutea on each ovary (number of corpora lutea on the left and the right ovary at puberty [**ORPL** and **ORPR**, respectively]) through laparoscopy.

A total of 74 L77 and 89 L98 gilts (2 to 3 gilts per litter) were then randomly chosen and kept for reproduction traits over up to 6 successive litters. They were managed under a batch farrowing system, with 3-wk intervals between successive batches. Gilts were submitted to a synchronization treatment with a progestagen to integrate farrowing batches. When estrus was detected, females were inseminated twice within a 12-h interval with semen from unrelated boars from the same experimental group. Females that were not pregnant after the first mating were allowed to rebreed 3 wk later but were culled if this second mating was unsuccessful. Three weeks after fertilization, ovulation rate at fertilization (**ORF** = ovulation rate of gestating sows) was estimated by measuring the number of corpora lutea on the left and right ovaries (ovulation rate at fertilization on the left and the right ovary [**ORFL** and **ORFR**, respectively]) through laparoscopy.

Females were then kept in collective pens and were fed 2.5 to 3 kg of a commercial sow diet during the whole gestation period. They were transferred to the farrowing unit 1 wk before the expected day of farrowing. They were placed in individual farrowing crates with slatted floor until weaning. Farrowing was induced with prostaglandin on the 113th day of gestation. The day of farrowing, the number of stillbirths (**SB**), the number of mummified piglets, and the number born alive (**NBA**) were recorded for each litter. All piglets born were individually weighed within 24 h after farrowing. All piglets from each farrowing batch were weaned on the same day at 4 wk of age. Sows were inseminated again on their first estrus after weaning.

Traits and Statistical Analyses

All above-defined sexual development traits, that is, TWI14, TWI18, TWI22, TWI26, BUL22, BUL26, TWESL, TLSL, TWISL, BULSL, BUWSL, and EPWSL for males and AGE PUB, BWPUB, ORP, ORPL, and ORPR for gilts, were analyzed using mixed linear models including herd, fattening batch within herd, and experimental group as fixed effects; birth litter as a random effect; and either BW (for all male traits) or age at measurement (for ORP, ORPL, and ORPR) as covariates using SAS (SAS Inst. Inc., Cary, NC) MIXED procedure. Contrary to Tribout et al. (2010), genetic relationships within groups were ignored, as preliminary analyses showed that results were very similar with or without considering these relationships.

Female reproduction traits included NBA, SB, the total number of piglets born per litter (total number born [TNB] = NBA + SB), and litter weight at birth (LWB), computed as the sum of individual piglet weights at birth, as well as components of litter size, that is, ORFL, ORFR, and ORF and prenatal survival rate (PSURV), defined as the ratio $PSURV = TNB1/ORF$, with TNB1 corresponding to TNB in the subset of litters with ovulation rate data. Additional traits, that is, interval from weaning to first estrus, farrowing interval, and length of productive life, computed as the period of time between first successful mating until last weaning, were also analyzed. These reproduction traits were analyzed using a mixed linear model including herd, farrowing batch within herd, experimental group, and parity as fixed effects and sow as a random effect. Litter weight at birth was analyzed with and without adjustment for TNB.

Table 2.1. Residual standard deviation for sow litter traits

Trait ¹	Experimental group ²		Pr > t for H0 : $\Delta G = 0$ ³
	L77	L98	
ORF	1.9 ± 0.26	2.1 ± 0.24	0.71
PSURV, %	13.8 ± 1.4	12.6 ± 1.2	0.50
TNB	2.3 ± 0.16	2.7 ± 0.15	0.12
SB	1.0 ± 0.14	1.3 ± 0.12	0.18
NBA	2.0 ± 0.15	2.7 ± 0.14	0.004
LWB, kg	2.5 ± 0.2	3.1 ± 0.2	0.03

¹ORF = ovulation rate at fertilization; PSURV = prenatal survival rate; TNB = total number born; SB = number of stillbirths; NBA = number born alive; LWB = litter weight at birth.

²L77 = experimental group produced by inseminating Large White sows with either stored, frozen semen from 17 Large White boars born in 1977; L98 = experimental group produced by inseminating Large White sows with semen from 23 Large White boars born in 1998.

³Probability (Pr) associated with the null hypothesis (H0): genetic trend (ΔG) = 0 (*P*-value) for each trait.

Interactions between fixed factors, in particular between experimental group and herd or parity, were tested in preliminary analyses. They were removed from final analyses when they were non-significant ($P > 0.10$) and had a limited effect on experimental group effects. The heterogeneity of variance across experimental groups (L77 vs. L98) was also tested in preliminary analyses using a likelihood ratio test. When variances were significantly different, the final analyses were performed using a model with different residual variances in L77 and L98 groups using the REPEATED statement of the SAS MIXED procedure.

The genetic trend (ΔG) and its SE for each trait was computed as (Smith, 1977)

$$\Delta G = 2 \times (\mu_{L98} - \mu_{L77}) \text{ and}$$

$$SE(\Delta G) = 2 \times SE_{L98-L77}$$

in which μ_{L98} and μ_{L77} are estimates of experimental group effects and $SE_{L98-L77}$ is the SE of the contrast between L98 and L77.

Table 2.2. Experimental group least-squares means and estimated genetic trend for boar sexual development

Trait ¹	Observations ²		LSM \pm SE ³		$\Delta G \pm SE^4$	Pr > t for $\Delta G=0^5$
	L77	L98	L77	L98		
TWI14, mm	93	110	69.0 \pm 0.7	70.9 \pm 0.7	3.8 \pm 2.0	0.07
TWI18, mm,	93	110	91.9 \pm 1.0	94.3 \pm 1.0	4.8 \pm 2.8	0.08
TWI22, mm	93	110	118.7 \pm 1.1	123.9 \pm 1.1	10.4 \pm 3.1	< 0.001
TWI26, mm	93	110	133.5 \pm 1.1	133.5 \pm 1.1	0.0 \pm 3.1	0.99
BUL22, mm	93	110	24.0 \pm 0.6	24.0 \pm 0.6	0.0 \pm 3.1	0.97
BUL26, mm	93	110	29.0 \pm 0.8	29.5 \pm 0.8	1.0 \pm 2.3	0.63
TWESL, g	57	65	313.9 \pm 8.4	332.1 \pm 7.7	36.4 \pm 22.8	0.11
TLSL, mm	36	41	122.2 \pm 1.7	127.7 \pm 1.5	11.0 \pm 4.5	0.02
TWISL, mm	36	41	78.3 \pm 1.05	79.8 \pm 0.93	3.0 \pm 2.8	0.29
BUWSL, g	55	64	92.7 \pm 4.6	86.2 \pm 4.3	-13.0 \pm 12.6	0.30
BULSL, mm	55	64	132.5 \pm 2.7	130.4 \pm 2.4	-4.2 \pm 7.2	0.55
EPWSL, mm	55	64	75.4 \pm 2.3	82.9 \pm 2.1	15.0 \pm 5.9	0.01

¹TWI14, TWI18, TWI22, and TWI26 = total width of testes at 14, 18, 22, and 26 wk of age, respectively; BUL22 and BUL26 = length of the bulbourethral gland at 22 and 26 wk of age, respectively; TWESL = testes weight at slaughter; TLSL = testes length at slaughter; TWISL = testes width at slaughter; BULSL = bulbourethral gland length; BUWSL = bulbourethral gland weight; EPWSL = epididymis weight.

²Number of observations per experimental group (L77 or L98). L77 = experimental group produced by inseminating Large White sows with either stored, frozen semen from 17 Large White boars born in 1977; L98 = experimental group produced by inseminating Large White sows with semen from 23 Large White boars born in 1998.

³Experimental group LSM and their SE.

⁴Estimated ΔG from 1977 to 1998 and its SE.

⁵Probability (Pr) associated with the null hypothesis (H0): $\Delta G = 0$ (P -value) for each trait.

RESULTS

Preliminary analyses showed no difference in residual variability between experimental groups for female and male sexual development traits. Conversely, as shown in Table 2.1, a significantly larger residual variability was observed in the L98 experimental group for some of the female productivity traits, that is, NBA and LWB. Although not significant, a similar tendency was observed for TNB ($P = 0.12$) and SB ($P = 0.18$), but no difference was observed for ORF or PSURV. Models with heterogeneous group variances were considered in final analyses for TNB, SB, NBA, and LWB. Preliminary analyses also showed that none of traits exhibited any experimental group \times herd interaction.

Male Traits

Results for male sexual development traits are shown in Table 2.2. Testes width of L98 males tended to be larger at both 14 and 18 wk of age and was significantly larger at 22 wk of age compared that of with L77 males. The situation was less clear at 26 wk of age and at slaughter: L98 boars had longer testes ($P = 0.02$) and a heavier epididymis ($P = 0.01$) at slaughter, but no difference was observed for TWISL or BULSL.

Female Traits

Results for gilt sexual development traits are given in Table 2.3. Age and BW at puberty were similar in the 2 experimental groups. Conversely, ORP was much larger in L98 gilts compared with L77 gilts, corresponding to a gain of more than 2 SD of the trait over 21 yr and an increase of 0.17 ± 0.06 corpora lutea/yr. The gain almost entirely resulted from an increase in the number of corpora lutea in the right ovary.

Table 2.3. Experimental group least-squares means and estimated genetic trend for gilt performance

Trait ¹	Observations ²		LSM \pm SE ³		$\Delta G \pm SE^4$	Pr > t for $\Delta G=0^5$
	L77	L98	L77	L98		
AGEPUB	72	84	218 \pm 4	215 \pm 4	5.8 \pm 7.0	0.49
BWPUB	72	85	131 \pm 4	136 \pm 3	9.5 \pm 6.6	0.15
ORP	43	51	15.5 \pm 0.5	17.3 \pm 0.3	3.6 \pm 1.3	0.009
ORPL	43	51	7.4 \pm 0.4	7.5 \pm 0.4	0.2 \pm 1.0	0.84
ORPR	43	51	8.1 \pm 0.4	9.8 \pm 0.4	3.4 \pm 1.0	0.001

¹AGEPUB = age at puberty; BWPUB = BW at puberty; ORP = ovulation rate at puberty; ORPL and ORPR = number of corpora lutea on the left and the right ovary, respectively, at puberty.

²Number of observations per experimental group (L77 or L98). L77 = experimental group produced by inseminating Large White sows with either stored, frozen semen from 17 Large White boars born in 1977; L98 = experimental group produced by inseminating Large White sows with semen from 23 Large White boars born in 1998.

³Experimental group LSM and their SE.

⁴Estimated ΔG from 1977 to 1998 (ΔG) and its SE.

⁵Probability (Pr) associated with the null hypothesis (H_0): $\Delta G = 0$ (P -value) for each trait.

Results for litter traits and their components are shown in Table 2.4. The increase in ovulation rate after mating was even larger than at puberty ($+0.22 \pm 0.06$ corpora lutea/yr, leading to an increase of about 2.5 SD over 21 yr). Contrary to ovulation at puberty, the gain resulted into an increase of the number of corpora lutea in both left and right ovaries (43 and 57%, respectively, of the total gain). The increase in litter size at birth was rather large (2.6 total piglets born/litter, i.e., 0.12 ± 0.04 piglet/yr). Yet it corresponded to only 57% of the gain in ovulation rate, due to a tendency toward an increase in the number of dead embryos/fetuses (0.10 ± 0.06 /yr; $P = 0.11$). Piglet losses also tended to increase at farrowing (0.8 more stillbirths; $P = 0.09$), so that the gain in number

of piglets born alive/litter only reached 1.8 piglet/ litter (about 0.7 phenotypic SD) over the period of time considered. With a gain of about 1.8 phenotypic SD, the improvement in litter weight was much larger than the gain in litter size, as it combined an increase in both prolificacy and average piglet weight (0.13 kg; $P = 0.10$). As shown from adjusted litter weight results, half of the gain in litter weight is due to the increase in piglet weight.

Table 2.4. Experimental group least-squares means and estimated genetic trend for components of sow prolificacy

Trait ¹	Observations ²		LSM \pm SE ³		$\Delta G \pm SE^4$	Pr > t for $\Delta G=0^5$
	L77	L98	L77	L98		
ORF	125	149	17.0 \pm 0.8	19.3 \pm 0.7	4.6 \pm 1.4	0.001
ORFL	125	149	8.2 \pm 0.5	9.2 \pm 0.4	2.0 \pm 0.9	0.02
ORFR	125	149	8.8 \pm 0.5	10.1 \pm 0.5	2.6 \pm 0.9	0.006
DEADEF	125	149	5.0 \pm 0.5	6.1 \pm 0.5	2.2 \pm 1.3	0.11
PSURV, %	125	149	70.6 \pm 3.4	68.4 \pm 2.8	-4.4 \pm 5.4	0.34
TNB1	125	149	12.0 \pm 0.6	13.2 \pm 0.5	2.4 \pm 1.0	0.01
TNB	252	283	11.6 \pm 0.5	12.9 \pm 0.4	2.6 \pm 0.9	0.006
NBA	252	283	10.4 \pm 0.51	11.3 \pm 0.45	1.8 \pm 0.9	0.04
SB	252	283	1.2 \pm 0.24	1.6 \pm 0.20	0.8 \pm 0.4	0.09
PSB, %	252	283	8.7 \pm 2.0	10.7 \pm 1.7	4.0 \pm 3.2	0.23
LWB, kg	252	283	15.7 \pm 0.67	18.1 \pm 0.60	4.8 \pm 1.3	<0.001
LWB _{adj} , kg	252	283	14.0 \pm 0.41	15.2 \pm 0.37	2.4 \pm 0.7	0.001
APWB, kg	252	283	1.35 \pm 0.04	1.42 \pm 0.03	0.13 \pm 0.08	0.10

¹ORF = ovulation rate at fertilization; ORFL and ORFR = ovulation rate at fertilization on the left and the right ovary, respectively; DEADEF = number of dead embryos/fetuses; PSURV = prenatal survival rate; TNB1 = total number born in the subset of litters with ovulation rate data; TNB = total number born; NBA = number born alive; SB = number of stillbirths; PSB = percentage of stillbirths; LWB = litter weight at birth; LWB_{adj} = LWB adjusted for TNB; APWB = average piglet weight at birth.

²Number of observations per experimental group (L77 or L98). L77 = experimental group produced by inseminating Large White sows with either stored, frozen semen from 17 Large White boars born in 1977; L98 = experimental group produced by inseminating Large White sows with semen from 23 Large White boars born in 1998.

³Experimental group LSM and their SE.

⁴Estimated ΔG from 1977 to 1998 (ΔG) and its SE.

⁵Probability (P) associated with the null hypothesis (H0): $\Delta G = 0$ (P-value) for each trait.

Table 2.5 shows results for sow performance over productive life. Due to experimental constraints, age at first farrowing was rather high, particularly in L98 experimental group. L98 sows has a smaller interval from weaning to first estrus than L77 sows (-1.8 d; $P = 0.002$), but the interval from weaning to fertilization and the farrowing interval were similar in the 2 experimental groups. The length of productive life and, to a lesser extent, the overall sow longevity were much shorter in L98 sows. The estimated trend represented 1.2 farrowing intervals, that is, a decrease of more than 1 litter over the whole productive life. Consequently, numerical and weight productivities of the sows showed a sharp increase when expressed per year of productive life (+6.8 piglets, $P = 0.005$, and +11.4 kg of additional litter weight, $P < 0.001$). The trend was still positive but no longer significant

when expressed as total number of piglets born and as total litter weight produced over the whole productive life.

DISCUSSION

The objective of this study was to estimate the effects of selection for a large number of traits that are not routinely measured in breeding schemes using frozen semen. As discussed by Tribout et al. (2010), such designs are of particular interest to have a broader view of the consequences of selection and to detect unfavorable correlated trends that could impair the value of the selected population in the future. Indeed, the first results from this study have shown that selection has affected piglet maturity at birth (Canario et al., 2007b) and sow farrowing behavior (Canario et al., 2014b). Moreover, estimates are simple contrasts between levels of a fixed effect and, contrary to BLUP estimates of genetic trends, do not depend on the genetic parameters used as priors. Conversely, as results are based on comparisons at the beginning and the end of the period considered, they do not provide any information on the shape of genetic trends during that period.

Table 2.5. Experimental group least-squares means and estimated genetic trend for sow performance over productive life

Trait ¹	Observations ²		LSM ± SE ³		ΔG ± SE ⁴	Pr > t for ΔG=0 ⁵
	L77	L98	L77	L98		
AFF, d	74	88	421 ± 5	437 ± 6	31 ± 12.6	0.01
IWFE, d	95	94	5.5 ± 0.33	4.5 ± 0.25	-1.9 ± 0.6	0.002
IWF, d	136	131	19.2±3.4	14.6±3.3	-9.2±7.1	0.19
FINT, d	217	227	155 ± 5	154 ± 5	-2 ± 5	0.70
LPL, d	67	83	490 ± 34	402 ± 39	-186 ± 81	0.02
LONG, d	68	84	796 ± 34	724 ± 39	-142± 82	0.08
NUMPROD	74	88	25.3 ± 0.8	28.7± 0.8	6.8 ± 2.4	0.005
WTPROD, kg	74	88	35.5 ± 1.1	41.2 ± 1.1	11.4 ± 3.0	<0.001
TOTPB	74	88	37.4 ± 2.6	40.1 ± 2.4	5.4 ± 7.2	0.44
TWTPB, kg	74	88	51.0 ± 3.6	55.2 ± 3.3	8.4 ± 10.1	0.39

¹AFF = age at first farrowing; FINT = farrowing interval; IWFE = interval from weaning to first estrus; IWF = interval from weaning to fertilization; LPL = length of productive life; LONG = longevity (age at last weaning); NUMPROD = total number of piglets born per sow per year; WTPROD = total weight of piglets born per sow per year; TOTPB = total number of piglets born over sow productive life; TWTPB = total weight of piglets born over sow productive life.

²Number of observations per experimental group (L77 or L98). L77 = experimental group produced by inseminating Large White sows with either stored, frozen semen from 17 Large White boars born in 1977; L98 = experimental group produced by inseminating Large White sows with semen from 23 Large White boars born in 1998.

³Experimental group LSM and their SE.

⁴Estimated ΔG from 1977 to 1998 (ΔG) and its SE.

⁵Probability (Pr) associated with the null hypothesis (H0): ΔG = 0 (P-value) for each trait.

Estimates of genetic trends might also be biased by heterosis effects that could have appeared when mating G77 to “modern” sows. As discussed by Tribout et al. (2010), the lack of generation ×

experimental group interaction on growth traits, which are also potentially affected by non-additive gene effects, might be an indication that heterosis effects were absent or limited in this experiment.

The present study focused on components of sow lifetime productivity. It showed a rather large increase in litter size and litter weight over the period of time considered. “Modern” sows are able to carry up to term much larger and heavier litters. The increase in the number of piglets is due to an important correlative response in ovulation rate, which largely exceeds the increase in litter size. In spite of the greater heritability of ovulation compared with litter size (0.32 vs. 0.11, respectively, on average, in the literature; Bidanel (2011)), this trend might be seen as rather surprising given the moderate correlation between ovulation rate and litter size (0.32 on average; Bidanel (2011)). In most cases, the relative correlative response (R) on ovulation rate (R_{OR}) to selection for litter size (R_{LS} ; R_{OR}/R_{LS}) has been close to unity (Perez-Enciso and Bidanel, 1997). The large genetic trend observed might partly be explained by a greater heritability of ovulation rate and/or a larger genetic correlation in the French LW breed compared with average literature values. The only available estimates in French LW (Rosendo et al., 2007b) are close to literature means for heritability (0.33) but somewhat stronger for the genetic correlation with litter size (0.41). It may also arise from favorable genetic relationships with other traits considered in the breeding goal. Indeed, Young et al. (1977), Bidanel et al. (1996), and Rosendo et al. (2007a) reported favorable genetic relationships between ovulation rate and growth traits. Conversely, the few available estimates tend to show that ovulation rate is lowly correlated with backfat thickness, carcass composition, and meat quality traits (Rosendo et al., 2007a, 2010). As a consequence of this large increase in ovulation rate, embryo/fetal mortality tended to be greater in L98 sows compared with L77 sows ($P = 0.11$). This greater wastage is in line with the results of Bolet et al. (1986) in so-called “hyperprolific” Large White sows and of Johnson et al. (1999) in a composite Large White × Landrace population. Potential reasons for this increased embryo/ fetal mortality have been discussed in detail by Foxcroft (2012), who concluded that selection for prolificacy has resulted in an “imbalance between the number of ovulations and developing embryos in utero and functional uterine capacity to support the optimal development of surviving fetuses to term” (Foxcroft, 2012, p. 318).

The effects of selection for a breeding goal including TNB as a prolificacy indicator were not limited to the gestation period but were accompanied by an increase in SB. Biological causes for this increased mortality were investigated by Canario et al. (2007b) and Canario et al. (2014b), who showed that piglet maturity at birth as well as sow farrowing behavior have been changed by selection. From an applied perspective, it has been shown that replacing TNB with NBA in the

breeding goal is an effective way to prevent the increase in the proportion of stillbirths (e.g., Guéry et al., 2009).

The impact of selection on the other reproductive trait considered in this study, that is, male and female sexual development, was more limited. Age at puberty in gilts did not differ between experimental groups. Larger values were observed in L98 males for some male sexual development traits but differences were rather moderate. These low to moderate trends are consistent with expected trends based on literature values of genetic correlations between sexual development and both production and litter traits (Bidanel, 2011).

A major result of this study is the significant trend observed for the residual variability of litter traits, particularly NBA and LWB. Contrary to Johnson et al. (1999), the greater variance of litter size at birth does not result from an increased variability of ovulation rate but rather from the full expression of the variation in uterine capacity in L98 sows. In L77 sows, uterine capacity variation would be limited by the number of ova shed in a larger proportion of females. This increase in residual variance, which is likely to be genetically determined, might have unfavorable consequences on litter performance as well as on progeny growth during the suckling and even the postweaning periods (e.g., Sell-Kubiak, 2015). This can, in some sense, be considered an indicator of a greater sensitivity of “modern” sows to their environment, that is, reduced robustness.

Another important result is the unfavorable trend observed for the length of sow productive life and sow longevity. A reduced longevity has unfavorable economical, sanitary, and ethical consequences on piglet production (Serenius and Stalder, 2006). In this study, the impaired longevity of L98 sows has reduced by 35% their advantage over L77 sows in terms of lifetime piglet production. Longevity is considered an important component of robustness in livestock species (e.g., Hermesch et al., 2015; Rauw and Gomez-Raya, 2015). The decreased longevity observed in this study is another indication of unfavorable effects of selection on pig robustness. Including robustness traits in future pig breeding objectives therefore appears necessary to combine high production efficiency with healthiness, robustness, and adaptation to more variable environments.

Implications

This study showed that 2 decades of selection in a maternal line have resulted in large improvements of sow numerical and weight productivity at birth. However, these improvements were accompanied by unfavorable correlative responses for several traits, such as number of stillbirths, sow longevity, or residual variability of litter size and litter weight, which tends to indicate that selection has adversely affected sow robustness. They strongly suggest the necessity to include

robustness traits in future pig breeding goals. Yet further research is needed to better characterize the different components of robustness and their impact on pig productivity, welfare, and health to be able to define the most relevant breeding objectives for the future.

This study also showed the interest of an accurate evaluation of the consequences of selection. The use of frozen semen is an interesting but relatively late method to evaluate the effects of selection. The development of fine phenotyping tools should be of great interest to get a “real-time” evaluation of the consequences of selection for a number of traits that are not limited to the components of the breeding goal.

2.3. The effects of selection on French Large White performance during the suckling period

We showed in previous chapter that selection had resulted in large improvements in litter size and litter weight, but also resulted in more variable sow performance, a higher number of stillbirths and a reduced longevity, which could be indicators of a lower robustness of “modern” sows. The second paper analyses sow and piglet performance during the suckling period. In order to disentangle as much as possible the effects of selection on sow and litter performance, it was decided to set up a factorial design by exchanging, when it was possible, half litters between L77 and L98 sows. It was additionally suggested to try to homogenize litters to either 7 or 13 piglets in order to have litters with low or high competition between piglets. In practice, the design was somewhat too complex to be fully achievable. In particular, litter standardization to either 7 or 13 piglets could not be fulfilled, as shown in Figure 2.8. Crossfostering was more successful, as 156 of the 249 litters nursed by L77 sows, i.e. 63%, were mixed litters. Corresponding figures for L98 were 143 of 278 litters, i.e. 51%. In these mixed litters 43% of G77 and 41% of G98 piglets were crossfostered.

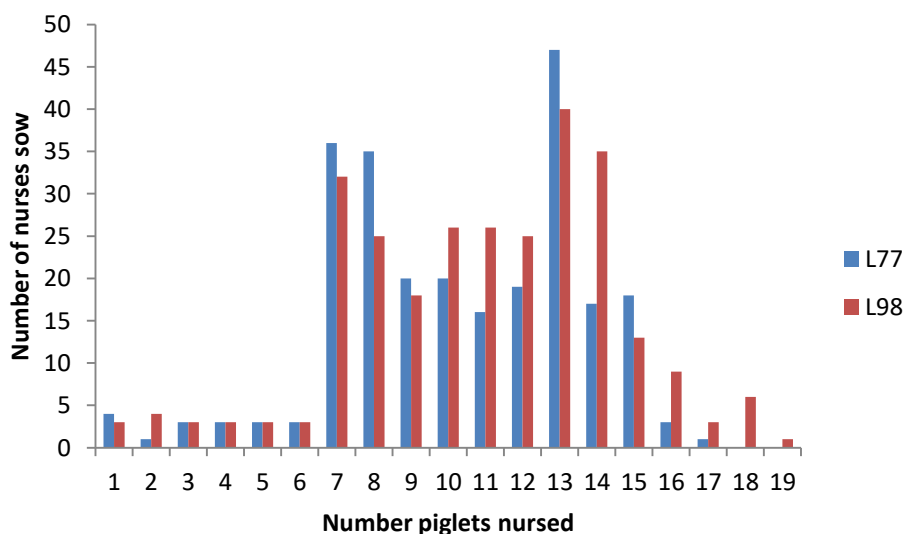


Figure 2.8. Distribution of litters according to the number of piglets nursed

Sow traits analyzed included numbers of piglets nursed at birth, at 3 weeks of lactation and at weaning at 4 weeks of lactation, as well as sow colostrum and milk composition traits. Sow milk production was also estimated from litter weight gain from birth to 21 days of lactation, provided that no creep feed is made available to piglets, which was the case in present study. Due to crossfostering and litter size standardization, litter size and weights are clearly different from what happened without crossfostering. They hence do not represent the capacity of L98 sows to maintain larger litters until weaning, but rather the comparative abilities of L77 and L98 sows to nurse similar

litters, i.e. independently from litter genotype, provided that there is no interaction with the potential effects of crossfostering. It would theoretically have been possible to go further by using mixed L77/L98 semen or embryo transfer in order to have mixed litters from the beginning of gestation. Mixed semen has recently been used to investigate piglet maturity between Large White and Meishan pig breeds. It gave quite interesting results in spite of the difficulty to control the relative proportions of the two litter genotypes (Canario et al., 2014b).

Some results such as the higher risk of mortality of G98 piglets during and shortly after farrowing were not unexpected based on previously known results. Potential causes of stillbirths have been discussed in previous chapter. Causes of early post-farrowing (i.e. before crossfostering) deaths include changes in sow behavior (Canario et al., 2014b), piglet colostrum intake (Decaluwe et al., 2014; Quesnel et al., 2015) as well as a potential lower maturity of G98 piglets (Canario et al., 2007b). Other results, e.g. the lower milk production of L98 sows, were more unexpected. Indeed, most studies report an increase in milk production over last decades (Mackenzie and Revell, 1998; Etienne et al., 2000). A favorable effect of selection on litter weight gain was obtained in sows from the third generation of this same experiment (Canario, 2006). Yet, these results are not necessary in contradiction. Litter size and genetic composition were similar in the current experiment, but are different in the above-mentioned results, where an increase in milk production associated with larger litters is expected.

The limited effects of selection on sow colostrum composition and on most sow milk components are in line with previous results reported by (Mackenzie and Revell, 1998). The only exception is milk fat content, which would mean a higher energy content of L98 sows' milk. If this is the case, the lower growth rate of piglets nursed by L98 would mean that the quantity of milk produced is lower than that expected on the comparison of litter weight gain. In any case, this result should be confirmed on a larger scale and the relationships between milk composition and the major traits in the breeding goal investigated.

The above-mentioned distribution of piglets according to sow experimental group has led us to consider six groups of piglets in preliminary analyses, i.e. G77 piglets nursed by L77 sows in unmixed (1) and mixed litters (2), G77 piglets nursed by L98 sows (3), G98 piglets nursed by L77 sows (4), G98 piglets nursed by L98 sows in unmixed (5) and mixed litters (6) – see table 2.9 for additional details. The effect of litter size on piglet weights and survival probability were considered in two different ways in preliminary analyses : 1) by considering small (≤ 10 piglets) vs large (>10 piglets); 2) by adding litter size as a covariate with a linear and a quadratic component and testing the homogeneity of the covariate across experimental groups. Similarly to litter size, piglet weight at

birth was introduced as a covariate with a linear and a quadratic component and its homogeneity tested across experimental group. These preliminary analyses quickly showed that: 1) there was no significant difference between piglets nursed by the same group of sows in mixed and unmixed litters, respectively; 2) when including the “small vs large” fixed litter effect jointly with litter size as a covariate, it never reached significance; 3) no heterogeneity of covariates across experimental group was detected. As a consequence, piglets from mixed and unmixed litters were grouped and the “small vs large” litter effect was removed from final analyses, and a single covariate was used across experimental groups.

Results also showed that selection has resulted in an increase in birth weight variability, both globally and within-litter, in the proportion of small piglets (less than 1 kg weight). This larger variability remains present until weaning. We will investigate in the next chapter the impact of this larger variability on the mean and variability of the performance of growing pigs.

Article 2 (submitted)

Estimation of the effects of selection on French Large White sow and piglet performance during the suckling period

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¹The financial support of the “Innovative actions” from the French Ministry of Agriculture is gratefully acknowledged. The authors thank the staff of INRA Bourges and GENESI experimental herds and of the laboratories implied in this experiment; special thanks are given to Francis Bussièrès for collecting, conditioning and taking care of boar frozen semen for more than 20 yrs.

²PS gratefully acknowledges the Directorate General of Human Resource for Science, Technology and Higher Education, Indonesia, Agreenium and INRA Animal Genetics Division for the financial support of the PhD thesis.

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ABSTRACT: The effects of 21 years of selection were estimated for sow and piglet performance during the suckling period in a French Large White (LW) pig population using frozen semen. Two experimental groups of pigs (EXP = L77 and L98) were produced by inseminating LW sows with either stored frozen semen from 17 LW boars born in 1977 (EXP = L77) or with semen from 23 LW boars in 1998 (EXP = L98). Seventy-four L77 and 89 L98 randomly chosen females were mated to, respectively, 15 L77 and 15 L98 randomly chosen boars for 6 successive parities. They produced a total of, respectively, 2796 G77 (L77 progeny) and 3529 G98 (L98 progeny) piglets including stillbirths. In order to disentangle direct and maternal effects on piglet growth, a 2 x 2 factorial design was set by cross-

fostering half litters across genetic groups the day after farrowing, resulting in mixed G77/G98 litters nursed by either L77 or L98 sows. Traits investigated included individual weight at birth (IWB), at 21d of age (IW21d) and at weaning at 4 wk of age (IWW), average daily gain from birth to 21 d of age (ADG21d) and to weaning (ADGBW), as well probability of stillbirth, of mortality on the first day post farrowing and from d2 to weaning, sow weight at farrowing and at weaning, sow feed intake, milk production, colostrum and milk composition. The variability of performance across genetic groups and litters was also investigated. The data were analyzed using generalized (piglet mortality) or standard mixed linear models (other traits). Results showed an increase in IWB (+240 ±72 g in 21 yr for IWB adjusted for total number born) and a negative maternal genetic trend was observed on piglet growth during the suckling period (e.g. -33 ±13 g/d in 21 yr for ADG21d, i.e. 14% of the mean), while direct genetic effects remained unchanged. Piglets nursed by L98 sows also had a 40% larger probability of being stillborn and a 28% larger probability of dying on d1, had a more heterogeneous IBW (358 g vs 336 g ; P < 0.001) and growth during the suckling period (60 g/d vs 56 g/d; P<0.001). L98 sows had a lower milk production than L77, but did not differ in weight, feed intake or colostrum composition. These results give evidence of negative correlated effects of selection for traits related to robustness.

Key Words: swine, genetic trend, frozen semen, piglet growth, piglet survival

Running head: Genetic trend estimation using frozen semen

Résumé : Les effets de 21 ans de sélection ont été estimés pour les performances des truies et des porcelets pendant la période d'allaitement dans une population porcine Large White française (LW) en utilisant de la semence congelée. Deux groupes expérimentaux de porcs (EXP = L77 et L98) ont été produits par l'insémination de truies LW avec, soit la semence congelée de 17 verrats nés en 1977 (EXP = L77), soit la semence fraîche de 23 verrats nés en 1998 (EXP = L98). Soixante-quatorze femelles L77 et 89 femelles L98 choisies au hasard ont été accouplées à, respectivement, 15 verrats L77 et 15 verrats L98 choisis au hasard pendant 6 portées successives. Elles ont produit un total de, respectivement, 2796 porcelets G77 (issus de L77) et 3529 porcelets G98 (issus de L98), y compris les mort-nés. Afin de dissocier les effets directs et maternels sur la croissance des porcelets, un dispositif factoriel 2 x 2 a été mis en place en pratiquant des adoptions croisées de demi-portées entre groupes génétiques le lendemain de la mise bas, ce qui a conduit à avoir des portées mixtes G77 / G98 nourries par des truies L77 ou L98. Les caractères étudiés incluaient le poids individuel des porcelets à la naissance (IWB), à 21 jours (IW21d) et au sevrage à 4 semaines d'âge (IWW), le gain moyen quotidien de la naissance, à 21 jours (ADG21d) et au sevrage (ADGBW), la mortalité au cours de la mise bas, du premier jour après la mise bas et du 2^{ème} jour au sevrage, le poids de la truie à la mise

bas et au sevrage, la consommation alimentaire de la truie, la production laitière, la composition du colostrum et du lait. La variabilité des performances entre groupes expérimentaux et entre portées a également été étudiée. Les données ont été analysées à l'aide de modèles linéaires mixtes généralisés (mortalité des porcelets) ou standards (autres caractères). Les résultats ont montré une augmentation d'IWB (240 ± 72 g en 21 ans en ajustant pour le nombre de nés totaux) et une évolution négative des effets génétiques maternels a été observée sur la croissance des porcelets pendant l'allaitement (e.g. 33 ± 13 g/j pour ADG21d, soit 14% de la moyenne), alors que les effets génétiques directs sont restés inchangés. Les porcelets nourris par les truies L98 présentaient également une probabilité 40% plus élevée d'être mort-nés et une probabilité 28% plus élevée de mourir le 1^{er} jour, étaient plus hétérogènes pour IWV (358 g vs 336 g, $P < 0,001$) et pour le gain moyen quotidien en allaitement (60 g/d vs 56 g/d, $P < 0,001$). Les truies L98 avaient une production laitière inférieure à celles de L77, mais ne présentaient pas de différence de poids, de consommation alimentaire ou de composition de colostrum. Ces résultats démontrent l'existence d'effets corrélés négatifs de la sélection pour les caractères liés à la robustesse.

Mots clés: porc, progrès génétique, semence congelée, croissance des porcelets, survie des porcelets

INTRODUCTION

Large improvements have been obtained in major pig populations for traits included in the breeding goal, i.e. growth, feed efficiency, carcass composition and, in maternal lines, sow prolificacy (Chen et al., 2002; Chen et al., 2003b; Tribout et al., 2010; Nielsen et al., 2013). Yet, selection potentially affects a much larger number of traits which are genetically correlated with the breeding goal. Correlated trends can be favorable - e.g. selection for feed efficiency results in decreased nitrogen and phosphorus excretion (Shirali et al., 2012; Saintilan et al., 2013) – but also sometimes detrimental. For instance, including the total number of piglets born in the breeding goal of pig dam lines has often resulted in an increase in the number of stillbirths (Canario et al., 2006; Su et al., 2007; Silalahi et al., 2016). Several authors have also suggested that selection for high production efficiency could increase sensitivity to environmental variations, i.e. decrease robustness (Phocas et al., 2014; Rauw and Gomez-Raya, 2015). These adverse effects are often difficult to detect when these correlated traits are not regularly recorded in breeding schemes.

The use of frozen gametes, most often semen, is a simple and rather powerful method to estimate genetic trends for a large number of traits (Smith, 1977). Its principle is to use the frozen material to produce a group of animals which can be used as an image of the population prior to selection and to compare the performance of these animals with another group of animals which is

representative of the population at the end of the period of time considered. A stock of frozen semen of French Large White boars born in 1977, constituted at the end of the 1970s, was used two decades later to estimate genetic trends for a large panel of traits. Results obtained for production traits, sow behavior and piglet maturity were reported by Canario et al. (2007a), Tribout et al. (2010) and Canario et al. (2014b). Silalahi et al. (2016) recently analyzed male and female sexual development, as well as litter size at farrowing, and showed that selection had resulted in a rather large increase in litter size, but also more variable sow performance, a higher number of stillbirths and a reduced longevity, which could be indicators of a lower sow robustness. The objective of this study is to estimate genetic trends on piglet and sow performance during the suckling period, with a particular attention to traits related to robustness.

MATERIALS AND METHODS

Animals

Animals used in this study were raised according to the protection of animals rules defined in the French law (Legifrance, 2016). French Large White (LW) sows born in 1997-98 were inseminated in the INRA GENESI experimental unit (17700 Surgères) with stored frozen semen from either 17 boar LW born in 1977 (S77) or with life semen from 23 LW boars born in 1998 (S98). During the 1977-1998 period of time, the French LW population has been selected for growth rate, feed efficiency and carcass composition. Additional traits, i.e. meat quality and litter size were added to the breeding objective in 1985 and 1990, respectively (see Tribout et al., 2010 for additional details).

Thirty and 33 litters, respectively, were produced from S77 and S98 boars. Pigs from this second generation will be noted as L77 and L98. After weaning, half of piglets from each litter and sex were transferred to another INRA experimental herd located near Bourges (18520 Avord). Fifteen L77 and 15 L98 males, as well as 74 L77 and 89 L98 gilts, were randomly chosen on a within-litter basis (one male and 2-3 gilts/litter) among these 63 litters and kept for reproduction. Sows were allowed to produce up to 6 successive litters, but were culled in case of reproductive failure as described by (Silalahi et al., 2016). Sows were managed under a batch farrowing system, with three week intervals between successive batches. They were inseminated twice when estrus was detected with semen of boars from the same experimental group. They were then kept in collective pens until one week before the expected day of parturition and were fed 2.5 to 3 kg commercial sow diet during the whole gestation period. They were then transferred to the farrowing unit. They were weighed and placed in individual farrowing crates with slatted floors up to piglets weaning. Farrowing was induced with prostaglandin on the 113th day of gestation. The day of farrowing, total number born was

recorded for each litter. Piglets born in these litters are referred to as G77 and G98 animals (Tribout et al., 2010).

When possible (i.e. when L77 and L98 sows farrowed on the same day or at a one-day interval), piglets were cross fostered at about one day of age in order to have a 2 x 2 factorial design with mixed G77 /G98 litters nursed by either L77 or L98 sows so as to disentangle sow and litter effects on piglet growth. During lactation, sows were given a diet containing a minimum of 13.8 MJ DE, 160g CP and 7.6 g total lysine per kg. They were given an increasing quantity of feed from day one after farrowing to day 5. They were then fed semi-ad libitum on the basis of their feed consumption in the previous day. Sow feed intake was recorded volumetrically from farrowing to weaning at 4 weeks of age in GENESI experimental unit. Sows were weighed again at weaning.

Colostrum samples were collected at the birth of the first and the last piglet from each litter and 24 hours after farrowing. A milk sample was then collected 14 days after farrowing. All samples were collected after an oxytocin injection. Samples were analyzed to determine their dry matter (**DM**), crude protein (**PR**), lactose (**LACTO**) and fat (**FAT**) content. Crude protein content was calculated by multiplying the N content of colostrum and milk by a conversion factor of 6.25.

When piglets died, the date and, when known, the cause of death were recorded. Identified causes of death were stillbirth, crushing, general weakness and cannibalism. All piglets including stillborn piglets were individually weighed (**IBW**) within 24 hours after farrowing, i.e. before cross-fostering. Alive piglets were then weighed again at 21d of age (**IW21d**) and at weaning at 4 weeks of age (**IWW**). No creep feed was distributed to piglets before 21 d of age in order to accurately estimate sow milk production. After 21 d of age, they were given access to creep feed formulated to contain a minimum of 14.7 MJ DE, 174g CP, 14.7 g Lysine and 5.8 g methionine.

Traits and statistical analyses

Sow traits analyzed included number of piglets nursed by each sow at d1 after cross-fostering (**NNd1**), at d 21 (**NNd21**) and at weaning (**NW**), litter survival rate, computed as $\%SURV = 100 \times (NW : NNd1)$, litter weight, computed as the sum of individual piglet weights, at d1 (**LWd1**), at d 21 (**LWd21**) and at weaning (**LWW**), sow weight before farrowing (**SWF**) and at weaning (**SWW**), sow total weight loss (**STWL**) from farrowing to weaning, computed as $STWL = SWF - SWW$, sow net weight loss (**SNWL**) from farrowing to weaning, computed as : $SNWL = STWL - 0.3 - 1.329 * LWB$, where **LWB** = litter weight at birth (Dourmad et al., 1997), sow daily feed intake from farrowing to weaning (**DFI**), milk production (**MILKP**) estimated as $MILKP = [(4 * ADG21 - 39) * NNd21]$, where **ADG21** = piglets

average daily gain from birth to 21 d of age – see below). This equation is based on the milk dry matter (DM) prediction equation of (Noblet and Etienne, 1989) and a milk DM content of 18%, as suggested by Etienne et al. (2000). Analyses were performed using mixed linear models including herd, farrowing batch within herd, experimental group as fixed effects, sow as a random effect. **LWd1**, **LWd21** and **LWW** were analyzed with and without adjustment for litter size, i.e. **NNd1**, **NNd21** and **NW**, respectively. Analyses were performed using SAS MIXED procedure. Interactions between fixed effects were tested in preliminary analyses, but none of them reached significance ($P < 0.10$) or had any noticeable effects on experimental group effects. As in Silalahi et al. (2016), the heterogeneity of variances across experimental groups (L77 vs L98) was tested in preliminary analyses using a likelihood ratio test.

Piglet traits analyzed included: 1) mortality traits, i.e. stillbirth (**SB**), mortality on day one (**MORTd1**), i.e. before cross-fostering, and from day 2 to weaning (**MORTd2W**), as well as potential differences in major causes of mortality, i.e. crushing (**MORT_CR**) and general weakness due to chilling and starvation (**MORT_GW**); 2) traits related to piglet growth during the nursing period, i.e. **IBW**, **IW21d** and **IWW**, as well as average daily gain from birth to 21d of age (**ADG21d**) and from birth to weaning (**ADGBW**). Mortality traits were analyzed using generalized mixed models (GLMM) using the GLIMMIX procedure of SAS (SAS Inst., Cary, NC), whereas the MIXED procedure of SAS was used for growth traits. In both cases, the models used included experimental group, sex, herd, batch within herd and parity of the dam, as fixed effects, birth or nursing litter as a random effect and, in additional analyses, litter size and IWB as covariates. Two levels (L77 and L98) were considered for the experimental group effect for traits measured before cross-fostering. After cross-fostering, six levels were considered in first analyses: G77 piglets nursed by L77 sows in litters with only G77 piglets (unmixed litters – level 1), in mixed G77/G98 litters (level 2) or nursed by L98 females (level 3); G98 piglets nursed by L98 dams in unmixed (level 4) or mixed (level 5) litters, or nursed by L77 sows (level 6). These six levels were reduced to four levels when piglet nursed in mixed vs unmixed litters of the same sow group has similar performances.

Interactions between fixed effects, as well as the homogeneity of residual variance and regression coefficients across experimental groups, were tested in preliminary analyses using likelihood ratio tests. Interactions were kept in final analyses when they had a noticeable effect on experimental group effects. The homogeneity of within experimental group, within-litter and across parity residual variances were additionally tested from the analysis of residuals using a Fisher test. When variances were significantly different ($P < 0.05$), they were accounted for in experimental group comparisons. Estimated genetic trends (ΔG) and their standard errors (SE) for each trait were

computed as (Smith, 1977):

$$\Delta G = 2 \times (\mu_{L98} - \mu_{L77}) \text{ and } SE(\Delta G) = 2 \times SE_{L98-L77}$$

In which μ_{L98} and μ_{L77} are estimates of experimental group effects and $SE_{L98-L77}$ is the SE of the contrast between L98 and L77.

RESULTS

Experimental group least squares means (LSM) for sow traits are given in table 2.6 for litter size and weight), table 2.7. for litter survival, sow weight loss, feed intake and estimated milk production, and table 2.8 for colostrum and milk composition. No interaction nor variance heterogeneity was detected for any of sow traits, so that only main effects and an homogenous residual variance were considered in final analyses. LSM for litter size and weight (table 2.6.) largely depended on experimental management decisions, i.e. cross-fostering and litter size standardization, so that genetic trends could not be estimated for these traits. Results just indicate that the objective of similar litter performances in the two groups of sows were globally fulfilled, even if the number and the weight of piglets nursed by L98 was slightly superior at the beginning of the nursing period.

Table 2.6. Experimental group least squares means (LSM) for litter size and weight

Trait ¹	Observations ²		LSM (SE) ³		Pr > t for L98 - L77=0 ⁴
	L77	L98	L77	L98	
NNd1	249	278	10.5 (0.4)	11.0 (0.4)	0.17
NNd21	249	278	8.4 (0.3)	8.8 (0.3)	0.19
NW	249	278	8.3 (0.3)	8.7 (0.3)	0.20
LWd1, kg	249	277	14.9 (0.5)	15.3 (0.4)	0.29
LWd21, kg	228	255	53.6 (2.1)	54.2 (1.9)	0.67
LWW, kg	226	251	69.9 (2.5)	69.7 (2.1)	0.91

¹NNd1, NNd21 = number of piglets nursed at d 1 (after cross fostering) and at d 21, respectively; NW = number of piglets weaned; LWd1, LWd21, LWW = litter weight on day 1 (after cross fostering), at d 21 and at weaning, respectively;

²Number of observations per experimental group (L77 or L98). L77 = experimental group produced by inseminating Large White sows with either stored, frozen semen from 17 Large White boars born in 1977; L98 = genetic group produced by inseminating Large White sows with semen from 23 Large White boars born in 1998.

³Experimental group LSM and their SE.

⁴Probability Pr > |t| associated with the null hypothesis (H0) : L98 - L77 = 0

Results for litter survival, sow weight loss, feed intake and estimated milk production are given in table 2.7. The performances of the two groups of sows were very similar. The only significant difference (P < 0.05) was observed for sow total weight loss from farrowing to weaning. It was mainly due to the heavier litters farrowed by L98 sows, as sow net weight loss during lactation was similar in L77 and L98 sows. Results for colostrum and milk composition traits are given in table 2.8. The compositions of the colostrum at birth of the first piglet, of the last piglet and 24h after farrowing were almost identical in the two groups of sows. The composition of the milk of the two groups of

sows at 14 d of lactation did not differ in terms of protein and to a lesser extent, dry matter and lactose content, but the milk of L98 sows had a significantly larger fat content (P=0.03).

Table 2.7. Experimental group least squares means (LSM) and estimated genetic trend for litter survival, sow weight loss, feed intake and estimated milk production

Trait ¹	Observations ²		LSM (SE) ³		ΔG (SE) ⁴	Pr > t for $\Delta G=0$ ⁵
	L77	L98	L77	L98		
%SURV	249	278	81.8 (2.7)	80.6 (2.3)	-2.4 (7.1)	0.59
SWF, kg	201	212	292.0 (3.4)	297.0 (3.1)	10.0 (9.2)	0.20
SWW, kg	201	212	251.0 (3.5)	252.0 (3.2)	2.0 (9.5)	0.70
STWL, kg	201	212	40.6 (2.4)	45.3 (2.17)	9.4 (6.5)	0.03
SNWL, kg	201	212	19.2 (2.2)	20.9 (2.0)	3.4 (5.9)	0.40
DFI, kg/d	77	104	4.8 (0.2)	4.5 (0.2)	-0.6 (0.6)	0.25
MILKP, kg/d	228	255	7.72 (0.35)	7.86 (0.30)	0.3 (0.9)	0.59
MILKP _{adj} , kg/d	228	255	7.65 (0.30)	7.62 (0.26)	-0.1 (0.8)	0.89

%SURV = 100 (NW x NNd21) = litter survival rate from birth to weaning; SWF, SWW= sow weight before farrowing and at weaning, respectively; STWL, SNWL = sow total and net weight loss from farrowing to weaning, respectively; DFI = sow daily feed intake during lactation; MILKP = sow milk production, estimated as: MILKP = [4*ADG21(g/d-39)*NN21d]; MILKP_{adj} = MILKP adjusted for the number of piglet nursed.

²Number of observations per experimental group (L77 or L98). L77 = experimental group produced by inseminating Large White sows with either stored, frozen semen from 17 Large White boars born in 1977; L98 = genetic group produced by inseminating Large White sows with semen from 23 Large White boars born in 1998. 3Experimental group LSM and their SE.

³Experimental group LSM and their SE.

⁴Estimated genetic trend from 1977 to 1998 and its SE.

⁵Probability associated with the null hypothesis (H0) : $\Delta G = 0$ (P-value) for each trait.

Numbers of piglets, overall means and standard deviations for the piglet traits analyzed are given in tables 2.9. and 2.10., respectively. On a total of 6325 piglets born in the course of the experiment, 649, i.e. 10.3 %, were stillbirths. Stillborn piglets were not weighed in Bourges experimental unit at the beginning of the experiment, so that birth weights were available for 489 animals. A total of 1056 additional piglets, i.e. 18.6 % died from birth to weaning. Deaths mainly occurred from d1 to d4. Crushing and general weakness accounted for, respectively, 44 and 39% of deaths from birth to weaning. Male piglets were more numerous than females at birth and at weaning (54.2 and 53.6 % of weighed piglets, respectively), with a tendency towards a higher proportion of males in G98 than in G77 piglets (55.0 vs 53.2 % of piglets; P <0.15). Table 2.9. also details the results of piglet cross-fostering between experimental groups. Due to the spreading out of farrowings over several days in each farrowing batch, cross-fostering was not possible for all litters. L77 sows nursed mixed litters in 156 of the 249 litters produced, whereas their L98 counterparts nursed mixed litters in 143 of the 278 litters produced. Hence, thirteen L77 litters received G98 piglets without providing G77 piglets for cross-fostering. The average proportion of cross-fostered piglets was similar in mixed litter from the two groups of sows, with L77 females nursing 739 G98 vs 961 G77 piglets, i.e. 43% G98 cross-fostered piglets, and L98 females nursing 692 G77 vs 977 G98 piglets, i.e. 41% G77 cross-fostered piglets. Yet, the within-litter proportion of G77 or G98 cross-

fostered piglets ranged from 20 to 90%. In both experimental groups, cross-fostered piglets were on average slightly heavier at birth than non-cross-fostered piglets (+41 g and +50 g, respectively, for G77 and G98 piglets raised in mixed litters).

Table 2.8. Experimental group least-squares means and estimated genetic trend for colostrum and milk composition

Trait ¹	Observations ²		LSM (SE) ³		ΔG (SE) ⁴	Pr > t for $\Delta G=0$ ⁵
	L77	L98	L77	L98		
Colostrum DM content, %						
At birth of first piglet	26	27	24.9 (1.0)	23.7 (0.7)	-2.4 (1.7)	0.56
At birth of last piglet	26	24	23.2 (1.0)	23.4 (0.8)	0.4 (1.8)	0.98
24 h after farrowing	26	25	22.1 (1.0)	21.2 (1.0)	-1.7 (2.0)	0.81
Milk DM content at d14, %	25	27	19.5 (0.4)	20.0 (0.4)	1.0 (0.7)	0.35
Colostrum PR content, %						
At birth of first piglet	26	27	15.8 (0.7)	15.5 (0.6)	-0.5 (1.3)	0.76
At birth of last piglet	26	27	15.1 (0.7)	14.4 (0.6)	-1.4 (1.3)	0.42
24 h after farrowing	26	27	9.0 (0.8)	9.0 (0.8)	-0.0 (1.6)	0.98
Milk PR content at d14, %	25	27	5.0 (0.1)	5.0 (0.1)	0.0 (0.2)	0.94
Colostrum FAT content, %						
At birth of first piglet	26	27	5.0 (0.4)	4.3 (0.4)	-1.4 (0.8)	0.19
At birth of last piglet	26	27	4.5 (0.5)	4.4 (0.4)	-0.2 (0.9)	0.88
24 h after farrowing	25	25	8.0 (1.1)	7.7 (1.0)	-0.6 (2.0)	0.82
Milk FAT content at d14, %	25	27	7.2 (0.4)	8.4 (0.4)	2.3 (1.0)	0.03
Colostrum LAC content, %						
At birth of first piglet	22	24	3.6 (0.2)	3.6 (0.1)	0.0 (0.3)	0.90
At birth of last piglet	20	20	3.3 (0.2)	3.4 (0.2)	0.2 (0.4)	0.71
24 h after farrowing	19	20	3.5 (0.4)	3.4 (0.3)	-0.2 (0.7)	0.79
Milk LAC content at d14, %	7	8	4.8 (0.4)	5.7 (0.6)	1.8 (1.0)	0.21

¹DM = dry matter; PR = crude protein; FAT = fat; Lac = lactose.

²Number of observations per experimental group (L77 or L98). L77 = experimental group produced by inseminating Large White sows with either stored, frozen semen from 17 Large White boars born in 1977; L98 = genetic group produced by inseminating Large White sows with semen from 23 Large White boars born in 1998.

³Experimental group LSM and their SE.

⁴Estimated genetic trend from 1977 to 1998 and its SE.

⁵Probability associated with the null hypothesis (H0) : $\Delta G = 0$ (P-value) for each trait.

The results of GLMM analyses of mortality traits are given in table 2.11. Three models are reported for each trait by successively adding LS and IWB as linear covariates to the first model.

Departures from linearity were tested in preliminary analyses by adding quadratic components (LS^2 and IBW^2) to the model. No noticeable departure from linearity was detected. Litter size had limited effects on mortality at all stages. An additional piglet in a litter did not change the risk of mortality on d1 and increased the risk of stillbirth or mortality from d 2 to weaning by only 2%. The influence of IWB was much stronger and highly significant. An increase in birth weight of 100 g decreased the probability of stillbirth, of MORTd1 and MORTd2W by 13%, 25% and 27%, respectively, consistent with the lower than average birth weights of stillborn piglets (1239 ± 43 g and 1335 ± 37 g, respectively, for G77 and G98) and from birth to weaning (1233 ± 43 g and 1241 ± 37 g, respectively, for G77 and G98), with no difference between MORTd1 and MORTd2W.

Table 2.9. Distribution of piglets according to mortality status, sow and piglet experimental group and sex

Trait	Sow experimental Group ¹	Piglet experimental group ¹						Total
		G77			G98			
		Females	Males ⁴	All	Females	Males	All	
Total born	All	-	-	2796	-	-	3529	6325
	W ²	1280	1453	2733	1544	1888	3432	6165
Stillbirths	All	-	-	272	-	-	377	649
	W ²	82	127	209	96	184	280	489
Birth to weaning	All	205	269	474	241	341	582	1056
Nursed piglets								
At birth	L77 (U) ³	405	443	848	-	-	-	848
	L77 (M) ³	400	561	961	421	321	742	1703
	L98 (U)	-	-	-	586	749	1319	1319
	L98 (M)	383	309	692	397	584	976	1668
At 21 days	L77	595	729	1324	378	292	670	1994
	L98	351	268	619	737	970	1707	2326
At weaning	L77	598	735	1333	361	266	627	1960
	L98	340	255	595	711	954	1665	2256

¹G77, G98 = experimental group of piglets produced by L77 and L98 sows, respectively; L77 = experimental group produced by inseminating Large White sows with either stored, frozen semen from 17 Large White boars born in 1977; L98 = experimental group produced by inseminating Large White sows with semen from 23 Large White boars born in 1998.

²W = number of animals with weight and sex information.

³U = unmixed litters: L77 sows nurse litters with G77 piglets only, L98 sows nurse litters with G98 piglets only. M = mixed litters: L77 and L98 sows nurse litters with both G77 and G98 piglets.

⁴Males were castrated 24 hours after birth.

The effects of adoption and of mixed vs unmixed litters were tested in preliminary analyses. Adoption appeared to have a strong effect on MORTd2W, with non-adopted piglets having a 138% higher risk of mortality than adopted piglets. Conversely, G77 or G98 piglets had a very similar risk of mortality when raised in mixed vs unmixed litters, so that no distinction between G77 or G98 mixed and unmixed litters was made in final analyses. G98 piglets had a 40% higher risk of being stillborn

($P < 0.12$) and a 28% higher risk of death on d1. Conversely, neither piglet nor sow experimental group had any effect on the risk of mortality after cross-fostering. Adjusting the data for litter size had a limited effect on the relative risk of mortality of experimental groups, while an adjustment for IWB strongly increased the risk of mortality of G98 piglets during farrowing and on d1 (+56% and +49%, respectively). Sex also strongly influenced mortality at all stages, with males being more at risk than females (+66%, +31% and +16%, respectively).

Table 2.10. Overall Mean and standard deviation for piglet weights

Trait ²	Sow experimental group ¹	Piglet experimental group ¹				Total	
		G77		G98		Mean	SD
		Mean	SD	Mean	SD		
IBW, g	All	1399	383	1431	407	1417	397
IBW, g (CF) ³	L77 (U) ⁴	1390	386	-	-	1390	386
	L77 (M)	1409	388	1508	341	1452	371
	L98 (U)	-	-	1405	422	1405	388
	L98 (M)	1450	341	1458	404	1454	379
IW21d, g	L77	6071	1562	6038	1535	6060	1552
	L98	5869	1594	6106	1671	6043	1654
IWW, g	L77	8058	1950	7896	1931	8006	1945
	L98	7784	2085	8036	2113	7968	2109

¹G77, G98 = experimental group of piglets produced by L77 and L98 sows, respectively; L77 = experimental group produced by inseminating Large White sows with either stored, frozen semen from 17 Large White boars born in 1977; L98 = experimental group produced by inseminating Large White sows with semen from 23 Large White boars born in 1998.

²IMB, IW21d, IWW = Individual piglet weight at birth, at 21 days of age and at weaning (at 28 days of age), respectively.

³CF = Individual birth weight of piglets of cross-fostered piglets in each experimental group.

⁴U = unmixed litters: L77 sows nurse litters with G77 piglets only, L98 sows nurse litters with G98 piglets only. M = mixed litters: L77 and L98 sows nurse litters with both G77 and G98 piglets.

Results of the analyses of residual variances of piglet growth traits are given in table 2.12. The residual standard deviation was much larger ($P < 0.001$) at birth in L98 than in L77 experimental group. This larger within-group variability is associated with a strong difference in within-litter standard deviation (34 g; $P < 0.001$). As a consequence, the average weight of the lightest piglet and the proportion of small piglets (<1 kg) in each litter were similar in L98 vs L77 litters (949 g and 25% in L98 vs 966 g and 26% in L77). Experimental group differences in IBW vanished after cross fostering, but piglets raised by L98 sows had more variable ADG21d and, consequently more heterogeneous weights at 21 d than piglets raised by L77 sows. This larger variability of L98 experimental group was also present, but was less pronounced, when considering ADGBW and IWW.

Table 2.11. Analysis of probability of piglets mortality traits: Odds ratio (OR) and significance of fixed effects and covariates

Trait ¹	Experimental group		Adoption		Sex		Parity	Herd	Batch	LS ¹		IWB ¹			
	OR _{EG} ²	Pr ³	OR _{AD} ²	Pr	OR _S ²	Pr				OR _{LS} ²	Pr	OR _{WB} ²	Pr		
Stillbirths	1.40	+	- ⁴	-	1.66	***	ns	*	+	-	-	-	-		
	1.34	ns	-	-	1.67	***	+	***	ns	1.02	ns	-	-		
	1.56	ns	-	-	1.76	***	+	***	+	0.97	ns	0.87	***		
MORTd1	1.28	***	-	-	1.31	***	ns	ns	ns	-	-	-	-		
	1.30	ns	-	-	1.31	+	ns	ns	ns	0.99	ns	-	-		
	1.49	+	-	-	1.45	*	ns	ns	ns	0.89	**	0.75	***		
MORTd2W	Sow		Piglet		2.38	***	1.16	+	***	ns	ns	-	-	-	-
	OR _{EG} ²	Pr	OR _{EG} ²	Pr											
	0.98	ns	1.02	ns											
	0.97	ns	1.02	ns	2.40	***	1.16	+	***	ns	ns	1.02	ns	-	-
	1.01	ns	1.15	ns	2.10	***	1.40	***	**	ns	ns	0.68	***	0.73	***

¹MORTd1 = mortality on d1 ; MORTd2W = mortality from d2 to weaning; LS = litter size = total number born for stillbirths, number born alive for MORTd1 and number nursed for MORTd2W.

²Odds ratios = ratio of mortality probabilities: OR_{EG} = G98 vs G77 for Stillbirths and MORTd1 ; OR_{EG} = L98 vs L77 (sow) and G98 vs G77 (Piglet) for MORTd2W; OR_{AD}= adopted vs non adopted piglets; OR_S= males vs females; OR_{LS}= Effect of an increase in LS of one piglet; OR_{WB}= Effect of an increase in piglet birth weight of 100 g.

³Pr : Level of significance of likelihood ratio test : ns = P > 0.012; + = P < 0.12 ; * = P < 0.05; ** = P < 0.01; *** = P < 0.001

⁴Not included in the model

Experimental group least squares means for piglet growth traits are given in table 2.13. Though born in larger litters, G98 piglets tended to have a higher average birth weight than G77 piglets ($P < 0.10$). The advantage became significant ($P < 0.01$) when adjusting the data for litter size, corresponding to an estimated genetic trend of 240 ± 72 g over 21 years. Adjusting the data for litter size had a much more limited effect on experimental group least squares means for IW21d, IWW and, above all, ADG21d and ADGBW, while IWB strongly affected the results. Whatever the model considered, piglet experimental group (G98 vs G77) had rather limited and non-significant effect on piglet growth traits, whereas sow experimental group had a strong influence on IW21d, ADG21d and ADGBW and, to a lesser extent, IWW. Piglets nursed by L98 sows had significantly lower weights and growth rates than piglets nursed by L77 sows resulting in negative estimated genetic trends of -0.4 and -0.5 trait standard deviation for IW21d and ADG21d, respectively. Corresponding effects were slightly lower for IWW and ADGBW (0.25 and 0.32 trait SD, respectively). Adjusting the data for IBW reduced the estimated trend for IB21d (-0.24 SD), but led to increased trends for the three other traits (-0.32, -0.58 and -0.47 SD for IWB, ADG21d and ADGBW, respectively).

Table 2.12. Within experimental group and within litter residual standard deviation (RSD) for piglet growth traits in L77 and L98 experimental groups

Trait ²	Residual standard deviation ¹		P-value ⁴	
	L77	L98		
IBW, g ³	Within EXP	336	358	< 0.001
	Within litter	270	302	< 0.001
IBW (CF), g ³	Within EXP	319	328	0.17
	Within litter	255	264	0.14
IW21d, g	Within EXP	1166	1260	< 0.001
	Within litter	900	973	< 0.001
IWW, g	Within EXP	1591	1665	0.03
	Within litter	1266	1264	0.95
ADG21d, g/d	Within EXP	56	60	< 0.001
	Within litter	43	47	< 0.001
ADGBW, g/d	Within EXP	56	58	0.05
	Within litter	44	44	0.68

¹Residual standard deviation computed with a model including without random litter effect and with litter size as a covariate; L77 = experimental group produced by inseminating Large White sows with either stored, frozen semen from 17 Large White boars born in 1977; L98 = experimental group produced by inseminating Large White sows with semen from 23 Large White boars born in 1998.

²IWB, IW21d, IWW = Individual piglet weight at birth, at 21 d of age and at weaning (at 28 d of age), respectively; ADG21d, ADGBW = average daily gain from birth to 21 d of age and to weaning, respectively.

³CF = Piglet individual birth weight after cross-fostering.

⁴P value = Probability associated with the F test under null hypothesis $H_0 : \sigma^2_{L77} = \sigma^2_{L98}$

Table 2.13. Experimental group least squares means and estimated genetic trends for piglet growth traits from birth to weaning

Trait ¹	Covariates ²	L77 ³		L98 ³		ΔG (SE) - Pr ⁵			
		G77 ³	G98 ³	G77	G98	Piglets		Sows	
IWB, g	-	1430 (41) ⁴	-	-	1502 (33)	144 (86)		+	
	LS	1378 (35)	-	-	1498 (28)	240 (72)		**	
IW21d, g	Age	6441 (156)	6475 (161)	6027 (139)	6254 (122)	261 (290)	ns	-635 (291)	*
	Age, LS	6414 (156)	6446 (161)	6014 (139)	6225 (122)	243 (281)	ns	-621 (291)	*
	Age, LS, IWB	6233 (124)	6090 (123)	5887 (126)	6051 (122)	21 (243)	ns	-385 (243)	+
IWW, g	Age	8459 (172)	8429 (181)	8141 (167)	8251 (143)	80 (333)	ns	-496 (333)	+
	Age, LS	8426 (172)	8397 (181)	8102 (168)	8203 (144)	72 (334)	ns	-518 (334)	+
	Age, LS, IWB	8441 (166)	8168 (165)	7957 (169)	8016 (149)	-214 (325)	ns	-636 (325)	*
ADG21d, g/d	-	239 (7)	237 (7)	217 (6)	226 (5)	7 (13)	ns	-33 (13)	**
	LS	237 (7)	235 (7)	216 (6)	224 (5)	6 (13)	ns	-32 (13)	**
	LS, IWB	238 (7)	229 (7)	211 (6)	217 (5)	-3 (13)	ns	-39 (13)	***
ADGBW, g/d	-	247 (6)	243 (6)	233 (6)	235 (5)	-2 (11)	ns	-22 (11)	*
	LS	246 (6)	242 (6)	232 (6)	234 (5)	-2 (11)	ns	-22 (11)	*
	LS, IWB	250 (6)	240 (6)	230 (6)	230 (5)	-10 (10)	ns	-30 (10)	**

¹IWB, IW21d, IWW = piglet individual weights at birth, at 21 d of age and at weaning, respectively; ADG21d, ADGBW = piglet average daily gain from birth to 21 days of age and to weaning, respectively.

²Linear covariates included in the model of analysis

³G77, G98 = experimental group of piglets produced by L77 and L98 sows, respectively; L77 = experimental group produced by inseminating Large White sows with either stored, frozen semen from 17 Large White boars born in 1977; L98 = experimental group produced by inseminating Large White sows with semen from 23 Large White boars born in 1998.

⁴Experimental group least squares means and their SE.

⁵ ΔG (SE) = Estimated ΔG from 1977 to 1998 (ΔG) and its SE; Pr = Probability associated with the null hypothesis (H0) : $\Delta G = 0$ (P-value) for each trait : ns = P > 0.10 ; + P < 0.10; * P < 0.05; ** P < 0.01; *** P < 0.001.

DISCUSSION

The primary objective of the experimental program whose results are partly reported here was to estimate genetic trends for a large number of traits that are not routinely recorded in pig breeding schemes in order to get a more accurate knowledge of the effects of selection on major pig biological functions. It can be particularly useful to identify potential adverse effects of selection or suboptimal selection for some traits or biological functions. The comparison of new vs ancient samples of the

breed / population under study is a simple and elegant way to reach this goal. The ancient sample can be obtained by using stored frozen semen, embryos or other types of biological samples available in biological resource centers (e.g. (Bruford et al., 2015). As discussed by Tribout et al. (2010) and Silalahi et al. (2016), this type of experiment has many advantages including a great flexibility and the ability to provide estimates of genetic trends that do not depend on genetic parameter estimates. Conversely, it only provides two-points estimates of genetic trends and it requires to be carefully designed to avoid potential biases. This is particularly true for piglet pre-weaning traits, which depend on the genotypes of the sow and its piglets and on complex interactions between them. For instance, piglet growth is influenced by sow milk production capacity, milk composition, the number and the size of littermates, sow maternal as well as piglet suckling behavior.

The use a 2 x 2 factorial design and the homogenization of litter size between the two experimental groups has allowed to show that selection has mainly affected maternal genetic effects, while direct (piglet) genetic effects on pre-weaning growth have remained unchanged. The trend was negative for maternal genetic effects, particularly for ADG21d and IW21d, where piglets entirely depend on sow milk availability, which means that G98 sows had a lower potential to provide milk energy to their litter in response to a given demand from their piglets. As colostrum and milk composition have not changed during these 21 years (table 2.8), this implies that G98 sows have a reduced milk production as compared to their G77 counterparts. The lower difference observed when considering growth from birth to weaning is presumably due to the availability of creep feed during the fourth week of lactation, which is likely to soften differences in energy supply between litters. The 2 x 2 factorial design also allowed to show that both sow and piglet differences in mortality between d2 of lactation and weaning were limited. The existence of potential bias due to cross-fostering might be questioned. Indeed, adoptions were not fully at random, as: 1) the average birth weight of cross-fostered piglets was slightly heavier than within experimental group mean birth weight; 2) the probability of mortality in cross-fostered piglets was lower than in non-adopted piglets. Several arguments can be put forward to indicate that this is not the case. First, literature results tend to show that early cross-fostering has a limited effect on piglet performance (e.g. see (Heim et al., 2012). Then, the very similar effect of cross-fostering on mortality in L77 and in L98, as well as the lack of difference between the performance of mixed and unmixed piglets, tend to indicate that cross-fostering did not bias experimental group comparisons.

The current design did not allow to disentangle direct and maternal effects on stillbirths, early mortality and piglet birth weight. The use of mixed semen or mixed embryos from the two

experimental groups would have made it possible, as was successfully done in a comparison of piglet maturity around birth in Chinese Meishan and Large White pig breeds, even though controlling the relative proportions of the two populations was not straightforward (Canario et al., 2014a; Voillet et al., 2014). Yet, available results suggest that piglet birth weight and survival are to a large extent genetically controlled by maternal genes (Kaufmann et al., 2000; Su et al., 2008; Ibanez-Escriche et al., 2009a; Kapell et al., 2011; Banville et al., 2015), so that it may be hypothesized that genetic trends on these traits are to a large extent of maternal origin. However, when considered jointly, these trends are not so simple to understand, as an increase in birth weight is associated, at least at the phenotypic level, by a decreased risk of mortality. Previous results from this program have identified several potential causes for the increased risk of stillbirths and early mortality of G98 as compared to G77 piglets, i.e. a lower maturity of G98 piglets at birth (Canario et al., 2007a), a longer duration of farrowing (Canario et al., 2007b) and an impaired maternal behavior of L98 as compared to L77 sows (Canario et al., 2014a). The increased variability of litter weight at birth in L98 litters is likely to be an important additional factor contributing to the increased probability of mortality of G98 piglets, particularly on d1. Indeed, though heavier on average, L98 litters contain more heterogeneous piglets, so that the weight and proportion of small piglets are similar in L98 and L77, but small G98 piglets have to face an increased competition to the udder due to larger litters and heavier littermates, leading to an increased risk of mortality as compared to G77 piglets. This result is in line with genetic parameter estimates showing a genetic antagonism between within-litter variability in birth weight and survival (Damgaard et al., 2003; Huby et al., 2003; Bouquet et al., 2014), leading to the proposal of including variability traits in the breeding goal of pig dam lines (Bouquet et al., 2014).

Another noticeable result is the existence of a larger heterogeneity in the growth of piglets nursed by L98 sows as compared to L77 sows, although cross-fostering had removed the largest part of the heterogeneity between experimental groups on d1. This implies that L98 do not only have an adverse effect on average piglet growth rate, but also on the homogeneity of the piglet they nurse. The biological causes, as well as the potential impact of this larger heterogeneity on post-weaning growth, remain to be investigated.

IMPLICATIONS

This study investigated the consequences on the farrowing and nursing periods of 2 decades of selection for a combined breeding goal including growth, feed efficiency, body composition and litter size in a Large White dam line. The results provided evidence that the large improvements obtained for the traits included in the breeding goal have been accompanied by adverse effects on sow milk

production and on traits related to sow and piglet robustness (piglet mortality and heterogeneity of performance). They thus strongly suggest that future breeding goals should put more emphasis on sow maternal abilities and on traits related to robustness. Yet, further studies are necessary to investigate the biological bases of these adverse effects and their impact on the various components of sustainable pig production systems.

2.4. Effects of selection on the variability of growth and carcass performances

Results from the two previous chapters showed that selection in French Large White population has resulted in large improvements of sow numerical and weight productivity at birth. However, it was also accompanied by an increased variability of sow performance during farrowing and lactation. These results consequently encouraged looking at the effects of selection on post weaning performance and carcass traits. Indeed, this would allow to have a full picture of trends in the variability of slaughter pig performances during their whole life.

The major French payment systems currently encourage farmers to sell their pigs to slaughterhouses in a narrow range of slaughter weights to produce uniform carcass primal cuts which are easier to process. As farmers generally do not sell pigs every day, uniform slaughter weights will be favored by homogeneous post weaning performance. It is therefore important to know whether the increase in piglet weight variability during the suckling period influences the homogeneity of pig growth performance. More generally it is of interest to investigate the impact of the distribution of birth weight on subsequent performance, as several authors have reported significant effects of birth weight on subsequent growth performance (e.g. Milligan et al., 2001; Quiniou et al., 2002). Rehfeldt and Kuhn (2006) suggested that differences in birth weight would be associated with differences in the number of muscle fibers, which are formed prenatally. Gondret et al. (2004) showed that low birth weight piglets were 12 days older than their litter mates at the end of fattening and had a lower number of muscle fibers as compared to high birth weight piglets. Similarly, Fix et al (2010) showed a lower growth rate of light piglet at birth as compared to heavier piglets during all phase of production. Rehfeldt et al. (2008) reported optimal pork quality such as pH, intramuscular fat and lightness from middle-birth-weight pigs (1.23 to 1.53 kg). In contrast, Bérard et al. (2008) and Beaulieu et al., (2010) reported limited effect of birth weight on carcass, meat quality and eating quality of pork.

In this third paper, we first analyzed the residual standard deviations of pig performance from birth until slaughter and of carcass traits in order check whether selection has affected the variability of post-weaning growth and carcass traits. Then, correlations between residuals and within-litter standard deviations of birth and weaning weight with post-weaning growth traits and carcass residual traits were computed to investigate the impact of pre-weaning growth on post-weaning performance. Results showed that the variability of growth performance until slaughter was higher in G98 than in G77 pigs. Yet, the variability of pre-weaning traits was independent from that of post-

weaning traits. Birth and weaning weight had low to moderate effects on post-weaning growth, and there may be a slight increase in the correlation values over time. Results are detailed in article 3. This article is in preparation for submission to journal of animal science.

Paper 3 (in preparation)

Effects of selection and pre-weaning growth on the mean and variability of post-weaning growth and carcass performance of French Large White pigs¹

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¹ The financial support of the “Innovative action” from the French Ministry of Agriculture is gratefully acknowledged. The authors thank to the staff of INRA Bourges and GENESI experimental herds and of the laboratories implied in this experiment.

²PS gratefully acknowledges the Directorate General of Human Resource for Science, Technology and Higher Education, Indonesia, Agreenium and INRA Animal Genetics Division for the financial support of the PhD thesis.

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ABSTRACT; The focus of this work was to investigate the effects of 21 years of selection on the variability of post-weaning growth and carcass traits in French Large White (LW) pigs and to quantify the contribution of pre-weaning growth to this variability. Two experimental groups were produced by inseminating contemporary LW sows with either stored frozen semen from 17 LW boars born in 1977 (**S77**) or with semen from 23 LW boars born in 1998 (**S98**). A total of 30 L77 and 33 L98 litters were produced from S77 and S98 boars, respectively. Ninety gilts and 15 boars were chosen from each group and randomly mated within group for 6 successive parities. L77 and L98 sows produced a total of 252 and 283 litters, respectively, giving birth to 2,733 G77 and 3,432 G98 piglets. A total of 1,697 G77 and 1,920 G98 pigs were then performance tested. Pigs were measured for individual weight at birth (**IBW**), at weaning (**IWW**), at 10 weeks of age (**IW10W**), at 20 weeks of age (**IW20W**),

and at slaughter (**IWSL**, at about 105 kg live body weight), and for backfat thickness at 20 weeks of age (**ABT20W**). Average daily gain from weaning to 10 weeks of age (**ADG10W**) and from 10 to 20 weeks of age (**ADG20W**) were computed from weight measurements. All postweaning traits were analyzed using mixed linear models including the fixed effects of experimental group (EXP), sex, herd, batch, and the random effects of common litter and the homogeneity across experimental group of residual and within litter variances were tested. The influence of birth and weaning weight distribution was then investigated by computing correlations between residuals and between within-litter residual standard deviations of IBW and IWW with those of postweaning traits. Correlations were computed globally and in each experimental group to check potential differences between groups. Results showed a higher within experimental group and within-litter variance in G98 than in G77 pigs for all growth traits (+6 to +27%) and carcass weight, no difference between groups for carcass leanness traits and lower variances for ABT (-24%) for carcass fatness traits. Within experimental group, the variability of post-weaning traits was not related to the variability of piglet weight at birth and at weaning. IWB and IWW had moderate to low positive residual correlations with post-weaning growth, low negative residual correlations with backfat thickness. Residual correlations with growth traits did not differ between experimental groups for IBW, but tended to be higher in G98 than in G77 for IWW. The residual correlation with backfat was more negative for G98 than G77 for both IBW and IWW. Residual standard deviation (RSD) correlations of IBW and IWW with carcass traits were all close to zero. Residual standard deviations (RSD) at birth and at weaning were positively correlated with RSD at 10 weeks, but had close to zero correlations with later growth traits and backfat thickness. In conclusion, selection has resulted in an increase in the variability of growth traits and carcass weight, a decrease in the variability of fatness traits and has slightly changed residual correlations between traits.

Keywords: swine, frozen semen, genetic trend, performance traits, variability

Running Head: Variability of growth and carcass traits

Résumé ; L'objectif de ce travail était d'étudier les effets de 21 années de sélection sur la variabilité de la croissance après le sevrage et les caractéristiques de carcasse chez les porcs Large White français et de quantifier la contribution de la croissance avant le sevrage à cette variabilité. Deux groupes expérimentaux ont été produits par l'insémination de truies LW contemporaines avec, soit la semence congelée de 17 verrats nés en 1977 (S77), soit la semence fraîche de 23 verrats nés en 1998 (S98). Au total, 30 portées L77 et 33 portées L98 ont été produites à partir des verrats S77 et S98, respectivement. Quatre-vingt-dix truies et quinze verrats ont été choisis au hasard dans chaque groupe et accouplé intra-groupe pendant 6 portées successives. Les truies L77 et L98 ont produit 252

et 283 portées, respectivement, donnant naissance à 2733 porcelets G77 et 3342 porcelets G98. Un total de 1697 porcs G77 et 1920 porcs G98 ont ensuite été soumis à un contrôle de performance. Les animaux ont été mesurés pour les poids à la naissance (IBW), au sevrage (IWW), à l'âge de 10 semaines (IW10W), de 20 semaines (IW20W) et à l'abattage (IWSL, à environ 105 kg de poids vif), et pour l'épaisseur de lard dorsal à 20 semaines d'âge (ABT20W). Les gains moyens quotidiens du sevrage à 10 semaines d'âge (ADG10W) et de 10 à 20 semaines d'âge (ADG20W) ont été calculés à partir des mesures de poids. Tous les caractères post-sevrage ont été analysés en utilisant des modèles linéaires mixtes incluant les effets fixes du groupe expérimental (EXP), du sexe, de l'élevage, de la bande et les effets aléatoires de la portée de naissance. L'homogénéité des variances résiduelles entre groupes expérimentaux et entre portées a été testée. L'influence de la distribution des poids de porcelets à la naissance et au sevrage a ensuite été étudiée en calculant les corrélations entre les résiduelles et entre les écarts-types résiduels intra-portée d'IBW et d'IWW avec ceux des performances post-sevrage. Les corrélations ont été calculées globalement et dans chaque groupe expérimental pour vérifier les différences potentielles entre groupes. Les résultats mettent en évidence une variabilité intra-groupe expérimental et intra-portée plus élevée chez les porcs G98 que chez les G77 pour l'ensemble des caractères de croissance (+6 à +27%) et pour le poids de la carcasse, une absence de différence entre groupes pour les caractères de teneur en muscle de la carcasse et des variances plus faibles pour ABT20W (-24%) et pour les caractères d'adiposité de la carcasse. Intra-groupe expérimental, la variabilité des caractères après sevrage n'est pas liée à la variabilité des poids des porcelets à la naissance et au sevrage. IBW et IWW présentent des corrélations résiduelles positives faibles à modérées avec la croissance post-sevrage et une corrélation résiduelle faiblement négative avec ABT20W. Les corrélations résiduelles avec les caractéristiques de croissance après sevrage ne diffèrent pas entre groupes expérimentaux pour IBW, mais ont tendance à être plus élevées chez les porcs G98 que chez les G77 pour IWW. La corrélation résiduelle avec ABT20W était davantage négative pour G98 que pour G77 pour IBW et IWW. Les corrélations résiduelles entre IBW ou IWW et les caractères de carcasse étaient toutes proches de zéro. Les écarts-types résiduels (ETR) des poids à la naissance et au sevrage étaient corrélés positivement avec l'ETR à 10 semaines, mais présentaient des corrélations proches de zéro avec les caractères de croissance et ABT20W. En conclusion, la sélection a conduit à une augmentation de la variabilité des caractères de croissance et du poids de carcasse, une diminution de la variabilité des caractères d'adiposité et a légèrement modifié les corrélations résiduelles entre les caractères.

Mots-clés : porc, semence congelée, évolution génétique, caractères de production, variabilité

Introduction

Selection for production and reproduction traits has been very successful in increasing the efficiency of pig production over the last decades, resulting in large genetic gains for litter size, growth efficiency and carcass quality (e.g. Tribout et al., 2010; Nielsen et al., 2013; Silalahi et al. 2016). Yet, these favorable trends have been accompanied by detrimental effects on other economically important traits, such as an increase in the number of stillbirths (Canario et al., 20006; Silalahi et al., 2016) or a reduced length of productive life (Silalahi et al., 2016). Silalahi et al. (2016; 2017) also showed that selection has resulted in an increased variability of sow performance and of piglet weight at birth, which might indicate a higher sensitivity to environmental variations, in agreement with the findings of several other authors (e.g. Rauw et al., 1998; Phocas et al., 2014; Rauw and Gomez-Raya, 2015). The increased (within-litter) variability in piglet weight has been shown to be related to an increased proportion of small piglets (Milligan et al., 2001a; Quiniou et al., 2002) and a higher probability of stillbirth and birth to weaning survival (Huby et al., 2003). Changes in the distribution of piglet birth weight may also affect post-weaning performance until slaughter (Rehfeldt et al 2008; Beaulieu et al., 2010) and its variability. An increased variability at slaughter may be detrimental for farmers, with potential penalties on the price paid for its pigs, as well as for slaughterhouses, making it more difficult to provide homogeneous products to processing units. The objective of this paper is to investigate whether selection can affect the variability of post-weaning growth and carcass performances and whether it can be attributed to changes in the distribution of birth or weaning weights, using data from an experimental design aiming at estimating the effects of 21 years of selection in French Large White breed.

MATERIAL AND METHODS

Animals and data recording

Animals used in this study were raised and slaughtered according to the protection of animal rules defined in the French law (Legifrance, 2016). French Large White (LW) sows born in 1997-1998 were inseminated in the INRA GENESI experimental unit (17700 Surgères) with either stored frozen semen from 17 LW boars born in 1977 (S77 sires) or with fresh semen from 23 LW boars born in 1998 (S98 sires). During the 1977-1998 period of time, the French LW population has been selected for growth rate, feed efficiency and carcass composition. Additional traits, i.e. meat quality and litter size were added to the breeding objective in 1985 and 1990, respectively (see Tribout et al., 2010 for additional details).

Thirty and 33 litters were produced from S77 and S98 boars, respectively. Pigs from these litters were noted as L77 and L98, respectively. After weaning at 4 weeks of age, half of the piglets from each litter and sex were transferred to another INRA experimental herd located near Bourges (Avord 18520). Fifteen unrelated males and 90 females (2-3 gilts from each litter) from each of L77 and L98 experimental groups were then randomly chosen and kept for reproduction. They were mated within experimental group over up to 6 successive litters, producing a total of 252 L77 and 283 L98 litters. Females were managed under a batch farrowing system with 3 weeks' interval between successive batches. They were kept in collective pens until one week before the expected day of farrowing, and then transferred to the farrowing building and placed in individual farrowing crates. Piglets born in these litters are referred to as **G77** (offspring of L77) and **G98** (offspring of L98) experimental groups. The 2733 G77 and 3432 G98 piglets born were individually weighed at birth (**IBW**), at 21 days of age (**IW3W**) and at weaning (**IWW**). More details on this pre-weaning period can be found in Silalahi et al. (2017).

A total of 1697 G77 and 1920 G98 pigs were then performance tested in Le Magneraud and Bourges experimental herds between 10 weeks of age and 105 kg live weight as described by (Tribout et al., 2010). Pigs were raised in pens of 12 animals, where they were given ad libitum access to water and to a standard pelleted diet formulated to contain 3.200 DE/kg and 17% CP from 10 weeks of age until slaughter. Pigs were weighed individually at 10 weeks (**IW10W**) and at 20 weeks (**IW20W**) of age, and then the day before slaughter at 23 weeks of age on average (**IWSL**). Most pigs were also measured ultrasonically for backfat thickness at 20 weeks of age (**ABT20W**) at 6 locations (on each side of the spine, 4 cm from the mid-dorsal line at the shoulder, the last rib and the hip joint, respectively) using a real-time ultrasound Aloka SSD-500 device (Ecotro Aloka, Tokyo, Japan).

When reaching 105 kg live weight (**IWSL**), pigs were sent to commercial slaughterhouses. Carcasses were weighed after evisceration on the day of slaughter. The day after slaughter, carcass length was measured and a standardized cutting of the right half carcass was then performed in order to measure ham, loin, backfat, shoulder, belly and weights (see Tribout et al., 2010, for additional details).

Traits and statistical analyses

Growth traits analyzed were individual weights at 10 and 20 weeks of age and before slaughter (**IW10W**, **IW20W**, **IWSL**, respectively), as well as average daily gain (ADG) from weaning to 10 weeks of age (**ADG10W**) and from 10 weeks of age to 20 weeks of age (**ADG20W**). Carcass traits analyzed included average backfat thickness at 20 weeks of age (**ABT20W**), computed as the mean of the 6

ultrasonic backfat measurements, carcass weight (CWT), carcass length (CL) and estimated carcass lean content, computed from CGM probe measurements (Sydel, Lorient, France) using the equations of (Daumas et al., 1998), as well as carcass cut weights, i.e. ham (HAMWT), loin (LOINWT), shoulder (SHWT), Backfat (BFWT) and belly (BELWT) weights.

Trait variability was investigated from residuals of mixed linear model analyses using the same models as Silalahi et al. (2017) and Tribout et al. (2010) for pre- and post-weaning performances, respectively. They included the fixed effects of experimental group (G77 and G98), sex (female and castrate), herd (3 levels), fattening batch within herd (44 levels) and parity of the dam (for pre-weaning traits – 6 levels), birth or nursing litter as a random effect and age (live weight traits and ABFT20W) as a covariate. Weight was not included as a covariate for carcass traits, as the objective was to measure the observed variability on the slaughter chain. Details on the model used for each trait are given in Supplemental Table 1. The heterogeneity of variances across experimental groups (G77 vs G98) was tested in preliminary analyses using a likelihood ratio test. Residual values were then used to compute: 1) within experimental group and within litter standard deviations (WLS), 2) global and within experimental group residual correlations with the residual value of birth weight, global and within experimental group correlations with residual value of weaning weight. All the analyses were performed using the MIXED procedure of the SAS software (SAS Inst., Cary, NC).

Table 2.14. Number of observations, mean and standard deviation for growth and backfat thickness traits

Traits ¹	Observations ²		G77		G98	
	G77	G98	Mean	SD ³	Mean	SD ³
IBW _{pt} , g	1697	1911	1488	343	1517	354
IWW _{tot} , g	1928	2292	7973	1996	7996	2066
IWW _{pt} , g	1626	1816	8081	1927	8080	2019
IW10W, kg	1697	1920	26.2	6.0	26.9	6.2
IW20W, kg	1697	1920	97.2	11.7	97.0	14.3
IWSL, kg	1621	1826	104.8	5.6	106.4	6.4
ADG10W, g/d	1697	1920	424	112	438	110
ADG20W, g/d	1696	1919	847	123	891	142
ABT20W, mm	1281	1382	14.6	2.9	12.6	2.5

¹IBW_{pt}, IWW_{tot}, IWW_{pt}, IW10W, IW20W and IWSL = Individual weight at birth of performance tested pig, at weaning of all pigs (4 weeks of age), at weaning of performance tested pigs (4 weeks of age), at the beginning (at 10 weeks of age) and at the end of the performance test (20 weeks of age), and at slaughter respectively; ADG10W, ADG20W = average daily gain from weaning to 10 weeks of age and from 10 weeks to 20 weeks of age, respectively; ABT20W = average backfat thickness at 20 weeks of age; tot= all pigs; pt = performance tested pigs .

² number of observations for each experimental group; G77 is L77 offspring (L77 = experimental group produced by inseminating Large White sows with either stored, frozen semen from 17 Large White boars born in 1977); G98 is L98 offspring (L98 = experimental group produced by inseminating Large White sows with semen from 23 Large White boars born in 1998).

³ SD = standard deviation

RESULTS

The number of observations, mean and standard deviation of pig growth and carcass traits are given in tables 2.14. and 2.15. Birth weight was available on a total of 6,135 piglets. Among them, 4,220 piglets survived until weaning. Due to experimental constraints, only 1,697 piglets for G77 and 1920 piglets for G98 were performance tested until 20 weeks of age, 2,663 were measured for backfat thickness, 1,924 were measured for carcass traits and carcass cuts were available on 1,140 pigs. Performance tested pigs were supposed to be chosen at random among available piglets. This hypothesis was checked by comparing the distributions of weaning weights of the 4,220 weaned piglets and of the subset of 3,617 which were performance tested. Performance tested pigs were slightly heavier and less variable in both groups (means increased by 108 g and 80 g, respectively, and standard deviations decreased by 69 and 47 g, respectively, in G77 and G98). Changes were considered as limited and similar in both groups and it was hypothesized that their impact on the results was limited.

Table 2.15. Number of observation, means and standard deviation of carcass traits and carcass primal cuts

trait ¹	Observations ²		G77		G98	
	G77	G98	Mean	SD ³	Mean	SD
CWT , kg	856	1052	82.3	2.39	81.6	2.33
DP , %	866	1058	78.0	4.26	77.3	4.77
CL , mm	588	744	990	29.7	992.8	32.3
ECLC, %	481	550	56.6	3.94	59.8	2.88
Primal cut weight, kg						
HAMWT	519	621	9.46	0.91	9.86	0.89
LOINWT	517	622	10.2	1.02	10.8	1.04
SHWT	519	621	8.15	1.64	8.28	1.66
BFWT	517	621	3.35	1.15	2.84	0.92
BELWT	519	622	5.31	0.77	5.34	0.76

¹ CWT=carcass weight; DP= dressing percentage; CL = carcass length; ECLC = estimated carcass lean content; HAMWT = ham weight; LOINWT = loin weight; SHWT = shoulder weight; BFWT = Backfat weight; BELWT = belly weight.

² number of observation for each experimental group; G77 is L77 offspring (L77 = experimental group produced by inseminating Large White sows with either stored, frozen semen from 17 Large White boars born in 1977); G98 is L98 offspring (L98 = experimental group produced by inseminating Large White sows with semen from 23 Large White boars born in 1998).

³ SD = standard deviation

Within group (GRSD) and within litter (LRSD) residual standard deviations (RSD), as well as coefficients of variation (RSD / mean) for growth and fatness traits are given in table 2.16. Both GRSD and LRSD were significantly to highly significantly larger in G98 for all growth traits and lower for ABT20W. As shown by the increase in coefficients of variation, the largest part of the increased

variability was not due to a scale effect. It was mainly associated with a larger within-litter variability, as LRSD was comparable to GRSD for most traits.

Residual standard deviations and coefficients of variation for carcass traits are shown in table 2.17. They have been computed with and without adjusting for slaughter weight to compare the variability on the slaughter chain (unadjusted data) and on a standardized carcass (data adjusted to 105 kg live weight). Carcass weights of G98 pigs were more variable than those of G77 pigs. Yet, no other carcass trait, either unadjusted or adjusted to 105 kg live weight, appeared as more variable in G98. No difference of variability was observed for leanness traits (HAMWT, LOINWT, SHWT) and for carcass length, whereas a reduced variability was observed for fatness traits (BFWT, BELWT). Yet, the lower variability in G98 pigs was mainly a scale effect, as shown by the comparable CV values. Because of the lower variability of fatness traits, lower RSD and CV were also observed for ECLC.

Table 2.16. Within experimental group and within litter residual standard deviation (RSD) for post-weaning growth traits in G77 and G98 experimental groups

Trait ¹	Group	G77		G98		P-value ³
		RSD ²	CV, % ²	RSD	CV, %	
IW10W, kg	Within EXP	4.57	17.4	4.93	18.3	<0.01
	Within litter	3.82	14.6	4.06	15.1	<0.01
IW20W, kg	Within EXP	9.07	9.3	11.58	11.9	<0.001
	Within litter	8.25	8.5	10.48	10.8	<0.001
IWSL, kg	Within EXP	4.89	4.7	5.76	5.4	<0.001
	Within litter	4.37	4.2	5.13	4.8	<0.001
ADG10W,g/d	Within EXP	92	21.6	97	22.1	<0.10
	Within litter	75	17.6	79	18.0	<0.05
ADG20W, g/d	Within EXP	107	12.6	122	13.7	<0.001
	Within litter	95	11.2	110	12.3	<0.001
ABT20W, mm	Within EXP	2.11	14.6	1.60	12.7	<0.001
	Within litter	1.82	12.5	1.34	10.6	<0.001

¹IW10W, IW20W = at the beginning (at 10 weeks of age) and at the end of the performance test (20 weeks of age), respectively; ADG10W, ADG20W = average daily gain from weaning to 10 weeks of age and from 10 weeks to 20 weeks of age, respectively; ABT20W = average backfat thickness at 20 weeks of age;

²RSD = residual standard deviation; CV = coefficient of variation = RSD / Mean (* 100 when expressed in % of the mean); G77 is L77 offspring (L77 = experimental group produced by inseminating Large White sows with either stored, frozen semen from 17 Large White boars born in 1977); G98 is L98 offspring (L98 = experimental group produced by inseminating Large White sows with semen from 23 Large White boars born in 1998).

³P value = Probability associated with F test under the null hypothesis $H_0 : \sigma_{L77}^2 = \sigma_{L98}^2$

Correlations between within-litter residual standard deviations (LRSD) within each experimental group are given in tables 2.18. Correlations of LRSD of birth and weaning weights were positive with LRSD of weight at the beginning of the performance test, but were close to zero with average daily gain on-test, weight at the end of the test and backfat thickness. No difference was

observed between G77 and G98 on test growth, whereas a positive correlation ($r=0.12$; $P<0.01$) was found between SDIBW and SDIWSL. Correlations between LRSD of birth and weaning weight and LRSD of carcass traits were all close to zero and not significant (results not presented).

Correlations between residuals of IBW and IWW with post-weaning growth traits are given in table 2.19. Correlations were moderate for early post-weaning growth, low and significantly positive for on-test growth. Correlations were low and significantly negative (except for IBW in G77 group) for ABT20W. Correlation with IBW did not differ between experimental groups for growth traits, whereas significantly larger correlations were observed in G98 than in G77 for IWW and on-test traits, either positively (ADG10W, ADG20W, IWSL) or negatively (ABT20W). A similar tendency ($P<0.10$) was observed for early growth. Correlations between residuals of IBW or IWW and carcass traits were all not significant and will not be detailed.

Table 2.17. Within experimental group and within litter residual standard deviation for carcass traits in G77 and G98 experimental groups

Trait ¹	Group	Unadjusted					Adjusted for SLW				
		G77		G98		P value ³	G77		G98		P value ³
		RSD ²	CV ²	RSD	CV		RSD	CV	RSD	CV	
CWT, kg	Within EXP	3.84	4.7	4.21	5.2	<0.001	2.09	2.5	2.22	2.7	0.07
	Within litter	3.28	4.0	3.59	4.4	<0.001	1.85	2.3	1.83	2.2	ns
DP, %	Within EXP	2.22	2.8	2.15	2.8	ns	2.15	2.8	2.15	2.8	ns
	Within litter	1.99	2.5	1.80	2.3	<0.01	1.91	2.5	1.78	2.3	<0.05
CL, mm	Within EXP	28.5	2.9	27.5	2.8	ns	26.1	2.6	25.5	2.6	ns
	Within litter	23.1	2.3	22.4	2.3	ns	20.8	2.1	20.5	2.1	ns
ECLC, %	Within EXP	3.08	5.4	2.41	4.0	<0.001	3.09	5.5	2.39	4.0	<0.001
	Within litter	2.41	4.3	1.95	3.3	<0.001	2.39	4.3	1.94	3.2	<0.001
HAMWT, kg	Within EXP	0.61	6.4	0.62	6.3	ns	0.48	5.1	0.47	4.8	ns
	Within litter	0.48	5.1	0.50	5.1	ns	0.38	4.0	0.36	3.7	ns
LOINWT, kg	Within EXP	0.75	7.3	0.76	7.0	ns	0.61	6.0	0.65	6.0	ns
	Within litter	0.59	5.8	0.63	5.8	ns	0.48	4.7	0.52	4.8	ns
SHWT, kg	Within EXP	0.61	7.48	0.62	7.48	ns	0.51	6.3	0.50	6.0	ns
	Within litter	0.52	6.38	0.53	6.40	ns	0.43	5.3	0.42	5.1	ns
BFWT, kg	Within EXP	0.65	19.4	0.57	20.1	<0.001	0.61	18.2	0.52	18.3	<0.001
	Within litter	0.49	14.6	0.40	14.1	<0.001	0.45	13.4	0.37	13.0	<0.001
BELWT, kg	Within EXP	0.55	10.4	0.52	9.73	ns	0.47	8.9	0.41	7.7	<0.001
	Within litter	0.45	8.47	0.44	8.24	ns	0.39	7.3	0.34	6.4	<0.001

¹ CWT=carcass weight; DP= dressing percentage; CL = carcass length; ECLC,% = estimated carcass lean content; HAMWT = ham weight; LOINWT = loin weight; SHWT = shoulder weight; BFWT = Backfat weight; BELWT = belly weight.

² Residual standard deviation; CV = coefficient of variation = RSD / Mean (* 100 when expressed in % of the mean); G77 is L77 offspring (L77 = experimental group produced by inseminating Large White sows with either stored, frozen semen from 17 Large White boars born in 1977); G98 is L98 offspring (L98 = experimental group produced by inseminating Large White sows with semen from 23 Large White boars born in 1998).

³ P value = Probability associated with the F test under null hypothesis $H_0: \sigma^2_{L77} = \sigma^2_{L98}$

To further investigate the effects of birth and weaning weight on post-weaning performance, IWB and IWW were successively added in the linear model for growth traits. The effects appeared as rather limited. For instance, the effect of an increase of 100 g birth weight was 0.75 kg, 0.38 kg and 7.8 g/d, respectively, for IW10w, IW20W and ADG20W with a difference in the slope of the regression line of 0.04 kg, 0.09 kg and 0.37 g/d, respectively for G77 and G98.

Table 2.18. Correlations between residual standard deviation (RSD) of pig post-weaning growth and fatness traits with RSD of birth and weaning weights

Traits ¹	SDIBW ² , kg		Prob (G77=G98)	SDIWW ³ , kg		Prob (G77=G98)
	G77	G98		G77	G98	
SDIW10W, kg	0.11 + ⁴	0.13 *	0.84	0.42 ***	0.43 ***	0.87
SDIW20W, kg	-0.001 ns	0.04 ns	0.66	0.06 ns	0.03 ns	0.74
SDIWSL, kg	-0.07 ns	0.12 +	<0.05	0.03 ns	0.11 +	0.38
SDADG10W, g/d	-0.009 ns	0.09 ns	0.28	0.18 **	0.17 *	0.87
SDADG20W, g/d	0.001 ns	0.09 ns	0.33	0.05 ns	0.06 ns	0.87
SDABT20W, mm	0.07 ns	-0.02 ns	0.42	0.15 *	0.13 +	0.83

¹SDIW10W, SDIW20W, SDIWSL = residual standard deviation of Individual piglet weight at start and at the end control of performance test and at slaughter (at 105 kg body weight), respectively; SDADG10W, SDADG20W, and SDADGSL = residual standard deviation of average daily gain from weaning to 10 weeks, from 10 weeks to 20 weeks of age, and to slaughter, respectively; SDABT20W = residual standard deviation of average back fat thickness at 20 weeks of age .

²SDIBW = residual standard deviation of Individual piglet weight at birth, ; G77 is L77 offspring (L77 = experimental group produced by inseminating Large White sows with either stored, frozen semen from 17 Large White boars born in 1977); G98 is L98 offspring (L98 = experimental group produced by inseminating Large White sows with semen from 23 Large White boars born in 1998).

³SDIWW = residual standard deviation of Individual piglet weight at weaning, Prob (G77=G98) = probability associated with the test under the null hypothesis H0: $r_{G77}=r_{G98}$

⁴Superscript = Probability associated with the test under null hypothesis H0; r= zero; *** = <0.001; **= <0.01 ; *= <0.05; += <0.10 ; ns= >0.10

DISCUSSION

Results from previous experimental studies showed that selection had increase the variability of sow reproductive performance, i.e. litter size and weight (Silalahi et al., 2016), had a detrimental effect on sow nursing capacities and increased litter variability until weaning (Silalahi et al., 2017). The aim of this paper was to investigate whether the higher variability of piglet growth up to weaning affects post-weaning growth and carcass performances.

Our results showed that selection has resulted in a higher variability of post weaning growth until slaughter, which was associated with an increased variability of slaughter weight. Conversely, the reduction of carcass fatness has resulted in a decreased variability of fatness traits and of estimated carcass lean content. These results have some unfavorable impacts for farmers who will have increased difficulties to have all their pigs in the most favorable range of weights, particularly in all in all out systems (Merks et al., 2012; Sell-Kubiak et al., 2015), as well as for processing units, as a higher variability of body weight at slaughter is likely to increase processing costs (Hayenga et al.,

1985; Sell-Kubiak et al., 2015). Most literature results have concerned the pre-weaning period (Milligan et al., 2001b; Quiniou et al., 2002; Wolf et al., 2008; Silalahi et al., 2016). Our results tend to show that the variability of growth can be increased up to slaughter and that this variability is not only due to a scale effect. However, the increased variability of post-weaning growth may not be a simple effect of the increased variability at birth, as pre-weaning and post-weaning variabilities appear as uncorrelated. As suggested by Knap, (2005), it may indicate that selection has increased the sensitivity of animals to their environment, i.e. has reduced robustness.

Table 2.19. Residual correlations between pig post-weaning growth and fatness traits) and birth and weaning weights

Traits ¹	IBW ² , kg		Prob (G77=G98)	IWW ³ , kg		Prob (G77=G98)
	G77	G98		G77	G98	
IW10W, kg	0.436*** ⁴	0.443***	0.79	0.60***	0.64***	<0.10
IW20W, kg	0.23***	0.19***	0.17	0.23***	0.29***	<0.10
IWSL, kg	0.10***	0.15***	0.18	0.12***	0.19***	<0.05
ADG10W, g/d	0.31***	0.34***	0.32	0.30***	0.35***	<0.05
ADG20W, g/d	0.15***	0.14***	0.73	0.13***	0.19***	<0.05
ABT20W, mm	-0.03 ns	-0.12 ***	<0.05	-0.10***	-0.20***	<0.05

¹ IBW, IWW, IW10W, IW20W, IWSL = Individual piglet weight at birth, at weaning, at the beginning (at 10 weeks of age) and at the end of the performance test (20 weeks of age), and at slaughter, respectively; ADG10W and ADG20W = average daily gain from weaning to 10 weeks and from 10 weeks to 20 weeks of age, respectively; ABT20W = average back fat thickness at 20 weeks of age.

² IBW = Individual piglet weight at birth; G77 is L77 offspring (L77 = experimental group produced by inseminating Large White sows with either stored, frozen semen from 17 Large White boars born in 1977); G98 is L98 offspring (L98 = experimental group produced by inseminating Large White sows with semen from 23 Large White boars born in 1998).

³ IWW= Individual piglet weight at weaning.

Prob (G77=G98) = probability associated with the test under the null hypothesis H0: $r_{G77=G98}$.

⁴ Superscript = Probability associated with the test under null hypothesis H0; r= zero ; *** = <0.001; ** = <0.01 ; * = <0.05; += <0.10 ; ns= >0.10.

Our results have also shown that birth weight has moderate effects on early post-weaning growth and a low, but significant effect on growth up to slaughter, and that the effects tend to be larger in “modern” pigs. As suggested by Beaulieu et al., (2010), piglets with a low birth weight would have a lower number of muscle fibers, which might then restrict their growth until slaughter. Rehfeldt and Kuhn (2006) showed that larger birth weights have larger muscle fibers and perform better after weaning. The very limited effects of birth weight on carcass traits agrees with those of Bérard et al. (2008) and Beaulieu et al. (2010). Conversely, Fix et al., (2010) showed that heavier birth weight pigs tended to have increased backfat depth as well as linear and quadratic effects of birth weight on longissimus muscle area.

CONCLUSION

This study provides evidence that selection has increased the variability of post-weaning growth until slaughter and of carcass weight at slaughter. This increased variability is not a simple consequence of an increased variability at birth, but could be an indicator of a detrimental effect of selection on robustness. It is likely to have unfavorable consequences for farmers, as it may increase labor and decrease pig average selling price. Sell-Kubiak et al. (2015) showed that a 10% decrease of standard deviation of growth rate in a system with fixed age at slaughter would lead to a financial gain of 0.21 euro/pig. Avoiding this increased variability or even reducing it would thus be of interest for farmers for economic reasons. If a decreased environmental variability is associated with an increased robustness, it would be of high interest for the sustainability of pig production.

Table 2.20. Supplemental Table 1. Fixed effects (and their significance), covariates (and their significance), and random effects included in the models for different traits

Traits ¹	Fixed effects ² and significance ³	Covariates ⁴ and significance ³	Random effect ⁵
IWB	EXP***, SEXE***, PARITY ns, BATCH***	TNB***	Litter
IWW	EXP ns, EXPNOU*, SEXE ns, PARITY***, BATCH***	NB_D1***, Age_4W***	Litter
IW10W	EXP ns, SEXE ns, PARITY**, BATCH***	AGE_10W***	Litter
IW20W	EXP***, SEXE***, PARITY*, BATCH***	AGE_20W***	Litter
IWSL	EXP***, SEXE***, BATCH***, COMP***	AGE_SL***	Litter
ADG10W	EXP*, SEXE ns, BATCH***, parity**, COMP***	BWW***	Litter
ADG20W	EXP***, SEXE***, BATCH***, COMP***	BW10W***	Litter
ABT20W	EXP***, SEXE***, BATCH***, COMP***	BW20W***, AGE_20W***	Litter
DP	EXP***, SEXE***, BATCH***, SLHO***	BWSL***	Litter
ECLC	EXP***, SEXE***, BATCH*, SLHO+	BWSL***	Litter
CWT	EXP***, SEXE***, BATCH***, SLHO***	BWSL***	Litter
CL	EXP ns, SEXE***, BATCH***, SLHO**	BWSL***	Litter
LOINWT	EXP***, SEXE***, BATCH***, SLHO***	BWSL***	Litter
BFWT	EXP***, SEXE***, BATCH***, SLHO***	BWSL***	Litter
SHWT	EXP**, SEXE***, BATCH***, SLHO***	BWSL***	Litter
HAMWT	EXP***, SEXE***, BATCH**, SLHO***	BWSL***	Litter
BELWT	EXP**, BATCH***, SLHO***	BWSL***	Litter

¹IWW, BW10W, BW20W, BWSL = Individual piglet weight at weaning, at start control of fattening, at end control of fattening and at slaughters (at 105 kg body weight), respectively; ADGW, ADG10W, ADG20W, and ADGSL = average daily gain from birth to weaning, to start of fattening, to end of fattening, and to slaughters, respectively.

²EXP, SEXE, PARITY, BATCH, COMP, SLHO = fixed effects of experimental group, sexe of the pig, parity of the sow, farrowing and fattening batch, fattening building and slaughter house respectively.

³ p-value of F-test for fixed effects and covariates in a linear model: *** = P value <0.001; ** = p value <0.01; * = p value <0.05; + = p value <0.10; ns = P value >0.10 (non significant)

⁴ TNB, NB_D1, AGE_4W, AGE_10W, AGE_20W, AGE_SL, BWW, BW10W, BW20W, BWSL = total number born, number of piglets alive at day one, age at 4, 10, 20 weeks and at slaughter, body weight at weaning, at 10, 20 weeks and at slaughter respectively.

⁵ litter = random effects of common environment of birth litter

2.5. Influence of selection on sow macro-environmental effects on their offspring performance

We have shown in previous chapters that selection in Large White breed has resulted in an increased variability of pre- and post-weaning growth and carcass weight (Silalahi et al., 2016; Silalahi et al., 2017a; Silalahi et al., 2017b), which might be an indicator of a stronger sensitivity to environmental variations. Although the increased variability of post-weaning traits could not be related, at the phenotypic level, to the increased variability of piglet weights at birth and at weaning, these latter traits have been shown to influence post-weaning growth until slaughter, with a tendency towards large correlation in “modern” pigs (Silalahi et al., 2017b).

These changes in the distributions of piglet weights at birth and at weaning are largely due to the sow, which has a strong influence on her litter during gestation and lactation. For instance, sow maternal genetic effects explain 15-20% of the phenotypic variability of birth weight while direct effects of piglet genes explain only 3-5% of this variability. Sow environmental effects include micro-environmental effects which are approximately quantified through the common birth litter effect (which also include dominance genetic effects) and macro-environmental effects due to e.g. litter size, milk production, body weight ... Sell-Kubiak et al. (2012) showed that offspring performance can partly be attributed to its performance as a young gilt, referred to as sow historical features. The objective of this study was to investigate sow macro-environment effects (or sow historical features) on the performance of her progeny.

Paper 4 (in preparation)

Selection changes the effects of sow features on growth and carcass performance of their progeny

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¹ The financial support of the “Innovative action” from the French Ministry of Agriculture is gratefully acknowledged. The authors thank to the staff of INRA Bourges and GENESI experimental herds and of the laboratories implied in this experiment.

²PS gratefully acknowledges the Directorate General of Human Resource for Science, Technology and Higher Education, Indonesia, Agreenium and INRA Animal Genetics Division for the financial support of the PhD thesis.

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Abstract; The focus of this work was to analyze the influence of sow macro-environmental effects on the growth and carcass performance of their progeny after 21 years of selection. Two experimental groups (L77 and L98) were produced by inseminating contemporary Large White (LW) sows with either stored, frozen semen from 17 LW boars born in 1977 or with semen from 23 LW boars born in 1998. The first generation produced consisted of 30 L77 litters and 33 L98 litters. Ninety gilts and 15 boars were chosen from each group and randomly mated within each group for 6 successive parities. Pigs produced in this second generation (**G77** as the offspring of L77 and **G98** as the offspring of L98) were individually measured for weight at birth (**IBW**), at the age of 10 weeks (**IW10W**), of 20 weeks (**IW20W**), and at slaughter (**IWSL**; around 105 kg live body weight), as well as for average backfat thickness at 20 weeks of age (**ABFT20W**). Average daily gain from 10 to 20 weeks of age (**ADG20W**) and to slaughter (**ADGSL**) were computed from weight measurements. Carcass traits included dressing percentage (**DP**), carcass length (**CL**) and weight (**CWT**), backfat thickness at section edge of the carcass (**BTSC**), carcass primal cut weight and carcass lean content (**ECLC**). Traits were analyzed

using a “base” mixed linear model which included the fixed effects of experimental group (**EXP**), sex (**SEX**), herd, batch, and the random effects of common litter and residual. sow features i.e. weight at birth (**SIWB**), post-weaning average daily gain (**SADG**) and average backfat thickness at 22 weeks of age (**SBFT**), age (**AGEPUB**) and weight (**BWPUB**) at puberty, age at first farrowing (**AGEF**), gestation length (**GL**), litter size (**TNB, NBA**) and weight at birth (**LWB**), sow weight loss (**SWL**) and feed intake (**DFI**) during the suckling period were successively added to the “base” model as linear covariates, and their interaction with experimental group was tested. Positive effects of age and weight at puberty, of gestation length and of sow net weight loss during lactation with progeny growth were detected. Conversely, larger litter sizes were associated with decreased body weights up to slaughter. It has also been shown that selection can modify the sign or the magnitude of some macro-environmental effects, in particular for age at puberty and at first farrowing and gestation length.

Keywords: swine, frozen semen, genetic trend, performance traits, variability

Running Head: Sow effects on their progeny’s performance

Résumé : L’objectif de ce travail article était d’analyser l’influence des effets macro-environnementaux de la truie sur la croissance et les performances de carcasse de leurs descendants après 21 ans de sélection. Deux groupes expérimentaux (L77 et L98) ont été produits par insémination de femelles Large White (LW) contemporaines avec la semence congelée de 17 verrats LW nés en 1977 (S77) ou la semence fraîche de 23 verrats LW nés en 1998 (S98). La première génération produite était constituée de 30 portées L77 et de 33 portées L98. Quatre-vingt-dix truies et quinze verrats ont été choisis dans chaque groupe et accouplés au hasard au sein de chaque groupe pendant 6 portées successives. Les porcs produits dans cette deuxième génération (G77 et G98, issus des reproducteurs L77 et L98, respectivement) ont été individuellement mesurés pour le poids à la naissance (IBW) et à l’âge de 10 semaines (IW10W), de 20 semaines (IW20W) et à l’abattage (IWSL, à environ 105 kg de poids vif, ainsi que pour l’épaisseur de lard dorsal à 20 semaines d’âge (ABT20W). Le gains moyens quotidiens de 10 à 20 semaines d’âge (ADG20W) et à l’abattage (ADGSL) ont été calculés à partir des mesures de poids. Les caractères de carcasse incluaient le rendement (DP), la longueur (CL) et le poids (CWT) de la carcasse, l’épaisseur de lard dorsal au niveau de la section de la carcasse (BTSC), le poids des morceaux de découpe et la teneur en viande maigre de la carcasse. Les caractères ont été analysés à l’aide d’un modèle linéaire mixte «de base » qui comprenait les effets fixes du groupe expérimental (EXP), du sexe (SEX), du troupeau, de la bande et les effets aléatoires de la portée de naissance et de la résiduelle. Les caractéristiques de la truie, c’est-à-dire le poids à la naissance, le gain moyen quotidien après le sevrage (SADG) et l’épaisseur moyenne de lard dorsal à 22 semaines d’âge (SBFT), l’âge (AGEPUB) et le poids (BWPUB) à

la puberté, la durée de gestation (GL), la taille de la portée (TNB, NBA) et le poids à la naissance (LWB), la perte de poids (SWL) et la consommation alimentaire (DFI) de la truie en lactation ont été successivement ajoutés au modèle comme covariables, et leur interaction avec le groupe expérimental a été testée. Des effets positifs de l'âge et du poids à la puberté, de la durée de gestation et de la perte de poids net de la truie durant la lactation sur la croissance des descendants ont été mis en évidence. Inversement, des tailles de portée plus importantes ont été associées à une diminution du poids vif jusqu'à l'abattage. Il a également été montré que la sélection peut modifier le signe ou l'ampleur de certains effets macro-environnementaux, en particulier pour l'âge à la puberté et la première mise bas et pour la durée de gestation.

Mots-clés : porc, semence congelée, progrès génétique, caractères de production, variabilité

Introduction

Pig production and reproduction traits have been largely improved through selection over the last decades (e.g. Tribout et al., 2010; Nielsen et al., 2013; Silalahi et al., 2016). However, these favorable trends have been accompanied by adverse effects on some other economically important traits (e.g. Canario et al., 2006; Silalahi et al., 2016) and an increased variability of pre- and post-weaning growth and carcass performances (Silalahi et al., 2016; Silalahi et al., 2017a; Silalahi et al., 2017b), which might be an indicator a stronger sensitivity to environmental variations. Although the increased variability of post-weaning performances could not be related, at the phenotypic level, to the increased variability of piglet weights at birth and at weaning, these latter traits have been shown to influence post-weaning growth until slaughter, with a tendency towards large correlation in “modern” pigs (Silalahi et al., 2017b). These changes in the distributions of piglet weights at birth and at weaning are largely due to the sow, which has a strong influence on her litter during gestation and lactation. Sow environmental effects include micro-environmental effects which are approximately quantified through the common birth litter effect (which also include dominance genetic effects) and macro-environmental effects due to e.g. litter size, milk production, body weight ... Sell-Kubiak et al. (2012) showed that offspring performance can partly be attributed to its performance as a young gilt, referred to as sow historical features. The objective of this study was to estimate sow macro-environment effects (or sow historical features) on the performance of her progeny and to investigate whether selection has changed the magnitude of these effects.

MATERIAL AND METHODS

Animals and data recording

Animals used in this study were raised and slaughtered according to the protection of animal rules defined in the French law (Legifrance, 2016). French Large White (LW) sows born in 1997-1998 were inseminated in the INRA GENESI experimental unit (17700 Surgères) with either stored frozen semen from 17 LW boars born in 1977 (S77 sires) or with fresh semen from 23 LW boars born in 1998 (S98 sires). During the 1977-1998 period, the French LW population has been selected for growth rate, feed efficiency and carcass composition. Additional traits, i.e. meat quality and litter size were added to the breeding objective in 1985 and 1990, respectively (see Tribout et al., 2010 for additional details).

Thirty and 33 litters were produced from S77 and S98 boars, respectively. Pigs from these litters were noted as L77 and L98, respectively. After weaning at 4 weeks of age, half of the piglets from each litter and sex were transferred to another INRA experimental herd located near Bourges (Avord 18520). Pigs were fed ad libitum with a standard pelleted diet 3200-3300 kcal DE/kg from 10 to 22 week of age (Le Magneraud) or 26 weeks of age (Bourges). In both herds, they were individually weighed at 10 and 22 weeks of age (IB10W and IBW22W, respectively) and measured for backfat thickness at 22 weeks of age at 6 locations (on each side of the spine, 4 cm from the mid-dorsal line at the shoulder, the last rib and the hip joint, respectively) using a real-time ultrasound Aloka SSD-500 device (Ecotro Aloka, Tokyo, Japan). Puberty was checked from 150 to 260 d of age using both progesterone and estrus information in order to measure age (AGEPUB) and weight at puberty (BW PUB) as described by Silalahi et al. (2016).

Fifteen unrelated males and 90 females (2-3 gilts from each litter) from each of L77 and L98 experimental groups were then randomly chosen and kept for reproduction. They were mated within experimental group over up to 6 successive litters, producing a total of 252 L77 and 283 L98 litters. Females were managed under a batch farrowing system with 3 weeks' interval between successive batches. When estrus was detected, females were inseminated twice within a 12-h interval with semen from unrelated boars from the same experimental group. They were kept in collective pens and were fed 2.5 to 3 kg of a commercial sow diet during the whole gestation period. They were then transferred to farrowing building one week before the expected day of farrowing and placed in individual farrowing crates. The day of farrowing, the number of, mummified, stillborn (SB) and born alive (NBA) piglets were recorded for each litter. All piglets born were individually weighed within 24 h after farrowing. Sows were fed ad libitum from about day 5 of lactation and their feed consumption

was recorded daily (**DFI**). Weaning took place at four weeks of lactation. Sows were weighed again (**SWW**), transferred to the gestation building and inseminated again on the first estrus after weaning. Sows which were not pregnant after the first mating were allowed to rebreed three weeks later, but were culled when this second mating was unsuccessful.

Piglets born in these litters are referred to as **G77** (offspring of L77) and **G98** (offspring of L98) experimental groups. The 2733 G77 and 3432 G98 piglets born were individually weighed at birth (**IBW**) and at weaning (**IWW**). More details on this pre-weaning period can be found in Silalahi et al. (2017). A total of 1697 G77 and 1920 G98 pigs were then performance tested in Le Magneraud and Bourges experimental herds between 10 weeks of age and 105 kg live weight as described by (Tribout et al., 2010). Pigs were raised in pens of 12 animals, where they were given ad libitum access to water and to a standard pelleted diet formulated to contain 3.200 DE/kg and 17% CP from 10 weeks of age until slaughter. Pigs were weighed individually at 10 weeks (**IW10W**) and at 20 weeks (**IW20W**) of age, and then the day before slaughter at 23 weeks of age on average (**IWSL**). Most pigs were also measured ultrasonically for backfat thickness at 20 weeks of age (**ABFT20W**) at 6 locations (on each side of the spine, 4 cm from the mid-dorsal line at the shoulder, the last rib and the hip joint, respectively) using the above-mentioned ultrasound Aloka SSD-500 device.

When reaching 105 kg live weight, pigs were sent to commercial slaughterhouses. Carcasses were weighed after evisceration on the day of slaughter. The day after slaughter, carcass length and backfat thickness at the shoulder, last rib and hip joint at the sectioned edge of the carcass were measured. After chilling, backfat thickness between the third and fourth lumbar vertebrae (**G1**), between the third and fourth last rib (**G2**), as well as loin eye depth between the third and fourth last rib (**M2**) were measured using a CGM probe (Sydel, Lorient, France) as described by Daumas et al., (1998). A standardized cutting of the right half carcass was then performed in order to measure ham, loin, backfat, shoulder, belly, head, foot, leaf fat and diaphragm weights (see (Tribout et al., 2010), for additional details).

Traits and statistical analyses

Growth traits analyzed were individual weights at birth, 10 and 20 weeks of age and before slaughter (**IBW**, **IW10W**, **IW20W**, **IWSL**, respectively), as well as average daily gain from 10 weeks of age to either 20 weeks of age (**ADG20W**) or to slaughter (**ADGSL**). Carcass traits analyzed included average backfat thickness at 20 weeks of age (**ABT20W**), computed as the mean of the 6 ultrasonic backfat measurements, carcass length (**CL**) and backfat thickness (**G1** and **G2**), loin eye depth (**M2**),

as well as carcass cut weights, i.e. ham (**HAMWT**), loin (**LOINWT**), shoulder (**SHWT**), Backfat (**BFWT**) and belly (**BELWT**) weights.

The effects of sow macro-environmental effects were investigated by adding each of them as a covariate in the analyses of growth and carcass traits. Effects investigated were gestation length (**GL**), computed as the difference between the date of farrowing and the date of first insemination, total number born (**TNB**), number born alive (**NBA**), litter weight at birth (**LWB**), computed as the sum of individual piglet weights from the same litter at birth, sow weight before farrowing (**SWF**) and at weaning (**SWW**), sow net weight loss (**SNWL**) from farrowing to weaning, computed from sow total weight loss (**STWL = SWF – SWW**) and (**SNWL = STWL - 0.3 - 1.329 * LWB** - Dourmad et al., 1997). Young sow traits, i.e. age (**AGEPUB**) and body weight (**BWPUB**) at puberty as well as age at first farrowing (**AGEF**) were also considered.

The same mixed linear model as that used by Silalahi et al. (2017b) was considered as the “base” model for the analysis of growth and carcass traits. They included the fixed effects of experimental group (G77 and G98), sex (female and castrate), herd (2 levels), fattening batch within herd (44 levels) and parity of the dam (for pre-weaning traits – 6 levels) birth or nursing litter as a random effect and age (live weight traits and ABT20W) or weight (carcass traits) as covariates. The different macro-environmental effects were then added to the base model (1 at a time) as covariates, either globally or within-experimental group. Potential non-linearities between the covariate(s) and the trait analyzed were tested in preliminary analyses by adding a quadratic term to the model and by analyzing residuals.

RESULTS

Sow traits considered as macro-environmental effects were available on 75 L77 and 89 L98 females which produced 252 and 283 litters, respectively (table 2.20.). The number of measurements varied to some extent according to the trait. In particular, puberty was checked in Le Magneraud only, so that data was available on only half of the animals.

Results on the effects of sow macro-environmental effects on growth and carcass traits are given in table 2.21. and 2.22., respectively. Only sow traits with highly significant effects ($P < 0.001$) or affecting more than one progeny trait were considered in order to limit the number of false positive results. When the regression coefficient of sow trait on progeny performance did not differ between G77 and G98, a single coefficient of regression was reported. When the interaction between experimental group and the covariate was significant ($P < 0.10$), within-experimental group regression

coefficients were reported. No significant departure from linearity was detected for any of the trait x macro-environmental effect combination.

Table 2.21. Number of observations, means and standard deviation (SD) for sow litter performance and sow historical features

Traits ¹	Observations ²		L77		L98	
	L77	L98	Mean	SD ³	Mean	SD ³
Sow historical features						
AGEPUB, day	35	42	227	25	228	28
BWPUB, kg	35	42	136	15	141	20
AGEF, day	74	89	424	37	433	58
Sow litter performance						
TNB	252	283	11.1	3.5	12.6	3.9
LWB, kg	220	237	15.7	4.5	17.8	5.3
GL, day	252	278	113.4	1.3	113.5	1.2
SWF, kg	251	278	269	39	273	41
SWW, kg	228	253	233	38	230	37
STWL, kg	228	251	35.7	19.0	42.1	21.0
SNWL, kg	202	213	15.2	17.6	17.4	19.0

¹ IWB= Individual weight at birth; ADG22W= average daily gain from 10 to 22 weeks of age; ABFT22W= average backfat thickness at 22 weeks of age; AGE PUB = age at puberty; BWPUB= body weight at puberty; SWF = sow weight at farrowing; SWW= sow weight at weaning; STWL= sow total weight loss (sow weight at farrowing-sow weight at weaning); SNWL= sow net weight loss (STWL - 0.3 - 1.329 * LWB); GL= gestation length; AGEF = age at first farrowing; DFI= daily feed intake during lactation; TNB = total number piglets born; NBA= number of piglets born alive; LWB= litter weight at birth;

² Sow experimental group: L77= offspring of S77 boars and L98 = offspring of S98 sires.

³ SD= standard deviation

Sow age and weight at puberty affected several growth traits as well as M2 muscle depth, loin weight (BWPUB) and belly weight (AGEPUB). An increase in weight at puberty was associated with larger weights and growth rates in both experimental groups except birth weight in G77. Conversely, the effect of AGE PUB differed according to the group. AGE PUB did not affect progeny growth, M2 and belly weight in G77, while a positive regression coefficient (RG) of AGE PUB on weight at birth, at 10 weeks of age and at slaughter, as well as on ADGSL, and a negative RG on M2 and belly weight were observed. Heterogeneous regression coefficients on growth traits were also observed for age at first farrowing (AGEF), with negative effects of AGEF on growth in G77 and no or slightly positive effects in G98. No effect of AGEF on carcass trait was detected.

Table 2.22. Estimated effect (regression coefficients with SE) of sow features on post weaning performance of their offspring

Traits ¹	EXP ²	Estimated effect (SE) ³					
		IBW, g	IW10W, g	ADG20W, g/d	IW20W, g	ADGSL, g/d	IWSL, g
AGEPUB	G77	-1.0 (1.1)ns ⁴	-10(20)ns	ns	ns	-0.3(0.3)ns	-10(10) ns
	G98	2.6 (1.0)**	40(20)*	ns	ns	0.5(0.2)*	20(10)**
Prob (G77=G98)		0.01	0.05	-	-	0.04	<0.01
BWPUB	G77	-2.7(2.0) ns	Ns	0.7 (0.3)**	50 (20)*	0.5 (0.3)+	ns
	G98	2.2(1.5) ns	Ns				ns
Prob (G77=G98)		0.03	-	ns	ns	ns	-
SNWL	G77	ns	20 (10)*	ns	40 (20)**	ns	12(7)+
	G98	ns		ns		ns	
Prob (G77=G98)		-	Ns		ns		ns
GL	G77	0.05(0.01)	Ns	6.5 (3.5)+	510 (300)+	7.8 (3.6)	ns
	G98		Ns			-0.8(4.0)	ns
Prob (G77=G98)		ns	-	ns	ns	0.07	-
AGEF	G77	-1.1 (0.6)*	-8.6 (5.0)+	-0.4(0.1)**	ns	-0.3(0.1) *	ns
	G98	0.4 (0.5) ns		0.2(0.1)*	ns	0.1(0.1) ns	ns
Prob (G77=G98)		0.03	Ns	<0.001	-	<0.01	-
TNB	G77	-39.8 (2.9)***	-160 (50)***	-2.5 (0.8)***	-140 (50)**	-2.3(0.8)**	-10(60) ns
	G98						-150(50) **
Prob (G77=G98)		ns	Ns	ns	ns	ns	0.08
NBA	G77	-19.9(2.6)***	-70(50)+	-1.7(0.8)**	-80(50)+	-1.6(0.7)*	-20(60) ns
	G98						-130(50)*
Prob (G77=G98)		ns	Ns	ns	ns	ns	0.06

¹ traits; AGE PUB = age at puberty; BWPUB= body weight at puberty; SWW=sow weight at weaning; SNWL=sow net weight loss (STWL- 0.3 - 1.329 * LWB - Dourmad et al., 1997); GL= gestation length; AGEF = age at first farrowing; TNB = total number piglets born; NBA= number of piglets born alive.

² Source of variation; EXP= experimental genetic group; L77 = experimental group produced by inseminating Large White sows with either stored, frozen semen from 17 Large White boars born in 1977 the G77 was L77 offspring; L98 = experimental group produced by inseminating Large White sows with semen from 23 Large White boars born in 1998 then G98 was L98 offspring.

³= estimated effect and its standard error (SE); IBW, IW10W, IW20W and IWSL= individual weight at birth, at 10 weeks (start control of fattening), at 20 weeks of age (the end control of fattening) and at slaughters (around 105 kg of body weight) respectively; ADG20W and ADGSL = average daily gain from 10 weeks until 20 weeks of age and until slaughters.

Prob (G77=G98) = probability associated with the test under the null hypothesis H0: $r_{G77}=r_{G98}$;

⁴ Superscript = Probability associated with the test under null hypothesis H0; r= zero; ***= <0.001; **= <0.01 ; *= <0.05; += <0.10 ; ns= >0.10.

Table 2.23. Estimated effect (regression coefficients with SE) of sow macro-environment effects on carcass traits

Traits ¹	EXP ²	Estimated effect (SE) ³								
		G1, mm	G2, mm	M2, mm	CL, mm	ECLC, %	HAMWT (g)	LOINWT (g)	BFWT (g)	BELWT (g)
AGEPUB	G77	ns	0.01 (0.01) ₄ ns	ns	Ns	ns	ns	ns	ns	3 (1)**
	G98	ns	-0.02 (0.01)*	ns	Ns	ns	ns	ns	ns	-2(2) ns
	Prob (G77=G98)		0.09							0.03
BWPUB	G77	ns	ns	-0.02 (0.02)	Ns	ns	ns	-7 (4)+	ns	6 (3) *
	G98	ns	ns	0.03 (0.02)	Ns	ns	ns	7 (3)*	ns	-1(2) ns
	Prob (G77=G98)			0.06				0.008		0.05
SNWL	G77	-0.02 (0.01)*	-0.03 (0.01)*	ns	Ns	0.01 (0.01)ns	ns	ns	4 (2)*	ns
	G98	0.02 (0.01)*	0.01 (0.01)ns	ns	Ns	-0.02 (0.01)*	ns	ns	ns	ns
	Prob (G77=G98)	0.02	0.02			0.03			ns	
GL	G77	-0.51 (0.16)***	-0.44 (0.15)**	0.10 (0.23) ns	-1.30 (1.43) ns	0.57 (0.13)***	40 (30)ns	60 (40)ns	-.100 (40)**	-40 (30)ns
	G98	0.32 (0.18)+	0.23 (0.16) ns	-0.43 (0.25) +	4.61 (1.44)***	0.06 (0.13) ns	-30 (30) ns	-50 (40) ns	80 (40)*	50 (30)ns
	Prob (G77=G98)	<0.001	<0.001	0.08	<0.001	0.003	0.08	0.03	<0.001	<0.01
TNB	G77	ns	-0.06 (0.04)	-0.06 (0.08)	0.75 (0.33)	ns	ns	ns	ns	ns
	G98	ns	ns	0.16(0.07)	Ns	ns	ns	ns	ns	ns
	Prob (G77=G98)		ns	0.05						

¹ traits; G1=back fat thickness at the third and fourth lumbar vertebrae; G2= back fat thickness at the third and fourth last rib; M2= loin eye depth at the third and fourth last ribs ; CL=carcass length; ECLC = estimated carcass lean content (5.684+1.197% ham + 1.076% loin – 1.059% backfat); AGE PUB = age at puberty; BWPUB= body weight at puberty; SNWL=sow net weight loss (STWL- 0.3 - 1.329 * LWB - Dourmad et al., 1997); GL= gestation length; TNB = total number piglets born; HAMWT=ham weight; LOINWT=loin weight; BFWT= backfat weight; BELLWT= belly weight;.

² Source of variation; EXP= experimental genetic group; L77 = experimental group produced by inseminating Large White sows with either stored, frozen semen from 17 Large White boars born in 1977 the G77 was L77 offspring; L98 = experimental group produced by inseminating Large White sows with semen from 23 Large White boars born in 1998 then G98 was L98 offspring.

³ = estimated effect and its standard error (SE); IBW, IW10W, IW20W and IWSL= individual weight at birth, at 10 weeks (start control of fattening), at 20 weeks of age (the end control of fattening) and at slaughters (around 105 kg of body weight) respectively; ADG20W and ADGSL = average daily gain from 10 weeks until 20 weeks of age and until slaughters.

Prob (G77=G98) = probability associated with the test under the null hypothesis: H0: $r_{G77}=r_{G98}$.

⁴ Superscript = Probability associated with the test under null hypothesis H0; r= zero; *** = <0.001; ** = <0.01 ; * = <0.05; += <0.10 ; ns = >0.10.

Gestation length affected several growth traits and all carcass traits. A longer gestation was associated with larger weights at birth and at 20 weeks of age and had a positive effect on ADG20W in both groups. Gestation length also affected ADGSL, with a positive effect of GL in G77, but had no effect in G98. It was also related with a reduced backfat (i.e. G1, G2, BFWT, BELLYWT) and a larger ECLC in G 77, while it mainly affected carcass length and tended to increase backfat traits in G98.

Litter size had highly significant effects on early growth traits and affected growth up to slaughter in both groups of pigs. An increase in total number born of one piglet decrease birth weight by almost 40 g, by 160 g at 10 weeks of age and by about 0.15 kg at 20 weeks of age and at slaughter. A similar pattern, but with lower effects, was obtained for number born alive. The only tendency towards heterogeneous regression coefficients concerned weight at slaughter. No effect was observed in G77, while the negative effect observed at a younger age remained present until slaughter in G98. Significant and similar effects of sow net weight loss on post-weaning weights were observed in the two experimental groups. Heterogeneous effects on some carcass traits (G1, G2 and ECLC) were also observed: high losses were associated with a reduced backfat thickness in G77, while the reverse was true in G98.

DISCUSSION

The objective of this study was to quantify the effects of sow macro-environmental effects on the performance of their progeny until slaughter and investigate whether selection has affected the magnitude of these effects. Indeed, selection has largely modified sow characteristics. “Modern” L98 sows are more prolific, are leaner, have heavier piglets than their “old” L77 counterparts. Many associated changes have been highlighted regarding sow behavior (Canario et al., 2014b), length of productive life (Silalahi et al., 2016), nursing capacities and homogeneity of litters produced (Silalahi et al., 2017a). Selection has also been shown to produce a larger variability up to slaughter and has slightly increased the magnitude of relationships between pre-weaning and post-weaning performances (Silalahi et al., 2017b). These changes may have altered the environment sows provide to their offspring.

This study confirms the impact of some sow characteristics on their progeny performance. This influence is not limited to the pre-weaning period, but can affect piglet growth until slaughter and even carcass performances. The most important is undoubtedly on the negative effect of litter size on progeny growth during the pre- and post-weaning periods, in agreement with several other studies (e.g. Sell-Kubiak et al., 2012). The rather limited effects on carcass traits are also in line with several previous studies (Beaulieu et al., 2010; Bérard et al., 2008) which reported that litter size had

no or limited effects on carcass quality. Globally, in spite of the tendency observed for weight at slaughter, it can be considered that selection has not changed the magnitude of this effect. The effect of sow net weight loss was also positive in both experimental groups, higher weight losses being associated to higher growth rates, presumably as an indicator of an increased ability to mobilize body reserves to feed piglets.

Gestation length had positive effects on growth traits, except ADGSL in G98 sows. This result is in line with Sell-Kubiak et al. (2013) who showed that gestation length affected post weaning performance indirectly by higher birth weight. The effect was similar in the two experimental groups, i.e. remained unchanged by selection. The effect of selection was significant for carcass traits, with a significant interaction with experimental group. Longer gestations were associated with leaner carcasses in G77 piglets, while the reverse seemed to be true for G98. The causes of these changes remain to be investigated.

Age at first farrowing also changed between G77 and G98, with a negative effect on growth traits in G77 and G98 and a tendency towards positive effects in G98. The effects in G98 sows are similar to those reported by Sell-Kubiak et al. (2012) for age at first insemination. A significant difference between experimental groups was also observed for AGE PUB. Regression coefficients were positive in G98, while they were close to zero in G77. An increased age at puberty has several favorable effects for slaughter pig producers. Sexually immature gilts have leaner carcasses than mature gilts (Eliasson et al., 1991) and the risk of boar taint is reduced in entire males. The situation is somewhat different for piglet producers. A delay in puberty will increase age at first farrowing and consequently increase feed and labor costs. Selection for early puberty results in higher lifetime reproduction (Rozeboom et al., 1996; Tummaruk et al., 2001; Patterson et al., 2010). Nelson et al. (1990) showed that females with earlier puberty produced more litters per sow. Similarly, Legault et al. (1996) showed in crosses the early mature Chinese Meishan breed that gilts mated at 5 months of age had a higher longevity than those mated at 7 months of age. Yet, because of its opposite interest for piglet vs slaughter pig producers and because of the high cost of measuring puberty, AGE PUB is usually not considered in breeding goals.

CONCLUSION

This study has allowed to quantify the effect of several sow macro-environmental effects on the performance of their progeny. Positive effects of age and weight at puberty, of gestation length and of sow net weight loss during lactation with progeny growth were detected. Conversely, larger litter sizes were associated with decreased body weights at different ages. It has also shown that

selection can modify the sign or the magnitude of some sow effects. This was particularly true for age at puberty and at first farrowing and for gestation length. The biological mechanisms underlying these changes remain largely unknown and would require further studies.

3. - General discussion

The French Large White pig populations has mainly been selected on lean tissue growth and sow prolificacy over the 1977–98 period of time (Bazin et al., 2003; Tribout et al., 2004), so that the differences between G77 and G98 groups estimated in this study mainly reflect direct and correlated responses to selection on these two components. This study also showed the interest of an accurate evaluation of the consequences of selection by using frozen semen. This methodology has previously been used in French pig population to estimate genetic trends after 5, 10 and 20 years of selection, respectively (Molénat et al., 1986; Ollivier et al., 1991; Bazin et al., 2003). The objective of this thesis was to estimate Genetic trends after 21 years of selection for reproduction traits, in particular for female reproduction traits. A special attention was given to traits related to sow robustness, which is a critical point for the development of more sustainable pig production systems. We will discuss main results, their interest and their limits, as well as some potential strategies proposed to increase robustness.

3.1. Main results

The first study showed that 2 decades of selection in a maternal line have resulted in large improvements of sow numerical and weight productivity at birth. However, these improvements were accompanied by unfavorable correlative responses for several traits such as an increase in the number and proportion of stillbirths. A major result of this study is the significant trend observed for the residual variability of litter traits, particularly NBA and LWB. Another important result is the unfavorable trend observed for the length of sow productive life and sow longevity. In this study, the impaired longevity of L98 sows has reduced by 35% their advantage over L77 sows in terms of lifetime piglet production.

The second study showed an increase in individual weight at birth (IWB) (+240, ± 72 g in 21 yr for IWB adjusted for total number born) and a negative maternal genetic trend was observed on piglet growth during the suckling period (e.g. -33 ± 13 g/d in 21 yr for ADG21d, i.e. 14% of the mean). Piglets nursed by L98 sows also had a 40% larger probability of being stillborn and a 28% larger probability of dying on d1, had a more heterogeneous birth weight (358 g vs 336 g; $P < 0.001$) and growth during the suckling period (60 g/d vs 56 g/d; $P < 0.001$). L98 sows had a lower milk production than L77, but did not differ in weight, feed intake or colostrum composition. Another noticeable

result is the existence of a larger heterogeneity in the growth of piglets nursed by L98 sows as compared to L77 sows.

The third study showed a higher within experimental group and within-litter variance in G98 than in G77 pigs for all growth traits (+6 to +27%) and carcass weight, no difference between groups for carcass leanness traits and lower variances for ABT (-24%) for carcass fatness traits and estimated carcass lean content. Within experimental group, the variability of pre-weaning traits was not related to the variability of piglet weight at birth and at weaning. In conclusion, selection has resulted in an increase in the variability of growth and carcass traits and has slightly changed residual correlations between traits.

In the fourth study, we quantified the effects of sow macro-environmental effects (sow features) on progeny performances. Age and weight at puberty, age at first farrowing, gestation length, litter size at birth and sow weight loss during lactation affected progeny growth performance until slaughter but, with the exception of lactation length, had limited effects on carcass traits. Selection changed the sign and/or the magnitude of some sow features.

3.2. Experimental design

3.2.1. Relevance of the design

This thesis used data from a large experimental design which has allowed several studies involving a wide range of traits to be performed. Traits investigated included growth, feed intake and efficiency, carcass traits, stress response, sow behavior and piglet maturity at birth. These studies indicated that the design was suitable to accurately estimate genetic trends in French Large White Pig population. Within this thesis, male and female reproduction, robustness related traits, as well as some undesired effects of selection are additional information that complemented the results of previous studies. However, if this experimental design is suitable to measure cumulative effects of selection after a long period of selection, it gives rather late trends and does not provide any indication on the shape of genetic trends during the period considered. Estimated genetic trends using best linear unbiased prediction (BLUP) is more flexible to get short term and regular information on genetic trends. A current major limit is that it is in most cases limited to traits considered in the breeding goal or as selection criteria. The situation is likely to change in the future with the development of automatized, high density phenotyping, which will make it possible to estimate genetic trends for a much larger number of traits.

3.2.2. Models of analysis

In genetic evaluations, it is necessary to estimate as accurately as possible genetic parameters of selected traits. Indeed, estimates of breeding values are biased if incorrect genetic parameters are used. Additionally, all the phenotypic and pedigree data should be included in the analysis to get unbiased estimates of genetic trends. This is not the case when using frozen semen, as genetic trends are estimated as contrasts between average phenotypic values of two populations. It could have been possible to include the numerator relationship matrix in each experimental group as done by Tribout et al. (2010). In practice, using BLUP animal model vs the simpler models we used led to very similar results. This was the case because sires within each experimental group were not or were lowly related. It could theoretically have been interesting to use it in chapter 3.4 to more accurately separate genetic from environmental variation, but a comparison of the two models showed limited changes in practice.

3.2.3. Data gap

Many estimates of direct and correlated effects of selection described in the literature are coming from rather old data and experimental design with a limited size. The experimental design analyzed in this thesis has ended ten years ago. Breeding goals over the period considered evolved over time, but mainly focus on productive traits i.e. growth rate, feed efficiency lean meat content, meat quality and, during the 90's, sow prolificacy. In recent years, additional traits have been added to the breeding goal of French pig dam populations. Total number born has been replaced by number born alive and number of teats and birth weight homogeneity has recently been included as a selection criterion. These changes in the breeding goal have led to additional changes in the Large White population. It would have been useful to complement current study with more recent BLUP estimates of genetic trends using field data. This was initially planned in the thesis, but has not been possible due to lack of time. Yet, genetic trend through selection is a slow process, and many of the original results obtained remain relevant and give very useful information on key biological responses which have to receive a particular attention.

3.3. Robustness indicators

Some of the traits analyzed are referred to in the thesis as indicators of robustness. This is in particular the case for longevity, piglet survival and performance variability. These traits do not

correspond to the definition of robustness given by, e.g., Knap (2005), based on environmental sensitivity, so that the fact that they characterize or not robustness has to be discussed,

3.3.1. Environmental sensitivity

The base equation of quantitative genetics, i.e. $P = G + E$, where P, G and E are phenotypic, genetic and environmental values, respectively, often assumes that their variances are the same for all animals and that G and E are independent, i.e. that $\text{cov}(G,E) = 0$. There is a growing evidence that it is often an approximation, and that some families have higher environmental variances, i.e. are more sensitive to environmental variations. Sauvant and Martin (2010) suggested the use of the response of animals to environmental variations as indicators for animal sensitivity. The results from the present study provide evidence that selection has increased residual variance in many stages of pig production, i.e. at farrowing, during the nursing and post-weaning periods. Conversely no increase in the variability of carcass traits was detected. Yet, this variability was not observed over a large number of environments, as only 3 herds were involved. There was no difference in variance across herds, but G98 had more variable performance in the 3 herds, which may be interpreted as a lower robustness. Similarly, the increased variability of sows across parities can easily be interpreted as an increased environmental sensitivity. Moreover, this higher variability affects traits considered as indicators of robustness such as piglet mortality or longevity. The consequences of this larger variability are different according to the level considered. Yet, it strongly affects well-being (through piglet mortality, group behavior ...) and herd management at all stages of production.

Pre-weaning period

The first article showed that the residual variance of litter weight and litter size across parities were higher in “modern” sows. This increased variability affects both the sow and the litter. At the sow level, a succession of large and small litters can be more difficult to manage for both the sow and the farmer. A large mobilization of body reserves for some parities and a more limited one for other parities might be problematic for the sow and impair its longevity. At the farm level, a standardization of litters is required to optimize herd management and reduce litter mortality. This standardization is in most case performed through crossfostering. This results in increased labor and production costs. Moreover, both the nurse sows and the crossfostered piglets experience more welfare problems than in non-fostered litters (Sørensen et al., 2016). Hence, sows that are able to distribute their resources similarly from the first to the last parities are desired (Ocepek et al., 2016) and might be considered as robust sow.

Lactating sow and piglets

Within litter birth weight variability in 'modern' G98 pigs was significantly higher than in G77. It was then followed by a higher variability of growth rate and body weight at weaning. This higher variability was associated with higher of mortality probability in 'modern' sows. The higher variability during lactation increased unfair competition between small and big littermates to get the better udder and proper quantities of colostrum and milk. Birth weight variability could be caused by fetus competition during late of gestation (Père and Etienne, 2000). This result is in line with genetic parameter estimates showing a genetic antagonism between within-litter variability in birth weight and survival (Damgaard et al., 2003; Huby et al., 2003; Bouquet et al., 2014), leading to the proposal of including variability traits in the breeding goal of pig dam lines (Bouquet et al., 2014). Sow capacity to produce homogenous litter weight and size could be improved by selection (Damgaard et al., 2003). Considering birth weight standard deviation or coefficient variation in a breeding scheme could be a solution to produce homogeneous birth weight, but it should be carefully considered (Bouquet et al., 2014; Canario et al., 2010).

Growth pig

An increased variability at slaughter may be detrimental for farmers, with potential penalties on the price paid for its pigs, as well as for slaughterhouses, making it more difficult to provide homogeneous products to processing units (Hermesch et al., 2000b). This study shows a higher variability of growth until slaughter and of carcass weight. No difference in the variability of carcass cuts was observed, but it should be mentioned that slaughter weights were rather carefully controlled in experimental units and are likely to be less variable than in a standard production herd, so that differences in variability of slaughter weight would probably have been more pronounced in a commercial herd. This increased variability until slaughter was not related to the variability observed during early life, so that its causes remain somewhat unclear. Noting that there is an increasing demand for more uniformity in pork cuts from the slaughter houses, retail and consumers, Merks et al. (2012) considered that a decreased in variability of performance traits should be considered in a breeding goal. Yet, this would decrease the efficiency of selection for the other traits of the selection goal. Another option would be to use the above-mentioned careful control of slaughter weights. Such a control is time consuming if it is performed manually, but becomes rather easy using automatic weighing devices which are likely to generalize with the increasing use of precision farming. It would even become possible to predict slaughter weights / dates several days or weeks in advance. Yet, rather large herds are necessary to have the high frequency of slaughter date necessary for this accurate control of slaughter weights.

3.3.2. Longevity

The impaired longevity on modern type sow has reduced by 35% their advantage in term of lifetime piglet production. Yet in spite of their shorter productive live, 'modern type' sows produce more pigs than old type sows. A lower longevity leads to increased replacement rates in a farm. It is likely to be a costly procedure, to increase risks of disease transmission and to reduce the number of piglets born during sow lifetime. Sow longevity can be improved by selection (Serenius et al., 2006; Serenius and Stalder, 2006; Yazdi et al., 2001; López-Serrano et al., 2000). Amer et al. (2014) reported that in a maternal line index, longevity contributed 12.5 %. Serenius et al. (2006a) showed that a sow line which has been selected only for prolificacy had a longer lifetime, but had a slower growth and had a poor carcass quality. In addition, Sánchez et al. (2006) and Theilgaard et al. (2009) reported that rabbits selected for prolificacy were 1.3 more likely to be culled than rabbits selected for longevity. Selection for longevity has been shown to be successful in rabbits (e.g. Larzul et al., 2014a) without adverse effects on litter size and environmental sensitivity (Theilgaard et al., 2007; 2009) .

3.3.3. Stillbirth and pre-weaning mortality

This study provides further evidence that selecting for total number born strongly increases number born alive, but is also accompanied by a higher number of stillbirths. Moreover, probability of early pre-weaning mortality was higher in G98. Previous results from this program have identified several potential causes for the increased risk of stillbirths and early mortality of G98 as compared to G77 piglets, i.e. a lower maturity of G98 piglets at birth (Canario et al., 2007a), a longer duration of farrowing (Canario et al., 2007b) and an impaired maternal behavior of L98 as compared to L77 sows (Canario et al., 2014a). Several efforts have been done to decrease stillbirth and pre-weaning mortality. Selecting on NBA in French Large White and Landrace population has prevented from a further deterioration of farrowing survival (Guéry et al., 2009). Similarly, selecting on the number of piglets alive at day 5 after birth instead of total number born resulted in an improvement of pre-weaning survival in Danish Landrace and Yorkshire populations (Lund et al., 2002; Su et al., 2007; Nielsen et al., 2013). Birth weight homogeneity was suggested as a solution to reduced stillbirth and pre weaning mortality (Milligan et al., 2002; Damgaard et al., 2003). Other maternal criteria such as number of teats, milk production and maternal behavior might also be of interest to decrease piglet mortality (Rutherford et al., 2013; Canario et al., 2014b).

3.3.4. Milk production

This study provides evidence that selection had adverse effects on milk production at a given litter growth potential. As explained by Dourmad et al. (2010) sow productivity (litter size and litter weight) has increased, but its lactation feed intake has remained rather constant. As a consequence, increasing litter size results in a decrease in the amount of milk per piglet (Devillers et al., 2007). According to Prunier et al. (2010), selection for growth rate simultaneously with feed efficiency has increased sow maintenance requirements, which would affect milk production and be at the origin of the higher pre-weaning mortality. As discussed by Quesnel (2011) and Quesnel et al. (2012), colostrum consumption also affect piglet survival, and a minimum amount of colostrum in early life would be required to survive until weaning. Theil et al. (2014) and Vadmand et al. (2015) suggested that body weight, backfat and fat mobilization affect to some extent the colostrum production and neonatal survival of piglets. Thekkoot et al. (2016) showed there is opportunity to implement genomic selection to improve sow lactation performance. However, an unfavourable genetic correlation was found between growth rate and leanness of the young animal and disturbed milk production (Rydhmer et al., 2001).

3.3.5. Maternal abilities

Previous results from this program have identified an impaired maternal behavior of L98 as compared to L77 sows (Canario et al., 2014a). They showed that “modern” sows are more reactive to farrowing stress and would then be were less attentive to their piglets, which would increase the risk of piglet crushing. Selection for lean growth has decreased levels of corticosteroids in modern pigs, resulting in a higher sow anxiety (Foury et al., 2009; Mormède et al., 2011; Terenina et al., 2013). This study showed that, though cross-fostering had removed the largest part of the heterogeneity between experimental groups on day one after birth, the growth of piglets nursed by L98 sows was more heterogeneous than growth of piglets nursed by L77 sows. This implies that L98 sows do not only have an adverse effect on average piglet growth rate, but also on the homogeneity of the piglet they nurse.

3.4. Breeding for robust pig

Undesired effects of selection within French large white maternal lines as described previously had led breeders to change the breeding goal. Yet additional new criteria related to robustness

would be worth considering simultaneously to avoid further degradation of performance traits. In a practical commercial context, selection for robustness traits has to be in balance with selection for production traits. Several literatures reviewed how to produce robust animals, e.g. (Knap, 2005; Hermesch et al., 2015; Rauw and Gomez-Raya, 2015). Knap (2005) was among the first to consider as worthwhile to include robustness related traits in the breeding goal. In a recent review, Hermesch et al. (2015) concluded that including growing pigs robustness traits in the breeding goal has the potential to achieve an extra annual genetic gain from \$2-4 per pig. According to Knap (2005) robustness is defined “as pigs that combine high production potential with resilience to external stressors, allowing for unproblematic expression of high production potential in a wide variety of environmental conditions”. He proposed two major options to consider robustness, either to include directly robustness related traits in the breeding goal, or to select animals on the basis of their reaction norm.

3.4.1. Direct selection for robust pigs

Traits included in the breeding goal can be, but are not necessarily, those who are used to compute the aggregate estimated breeding value (EBV) which is the basis for ranking candidates to selection. Robustness related traits to be included in the breeding goal and as selection criteria have to be properly and accurately defined. If we consider that longevity is a robustness related trait, we might define, as in Knap (2005) and Amer et al (2014), longevity as the trait to be included in the breeding goal. If longevity is difficult to measure because dates are missing, it can be replaced by number of parities produced by the sow as a selection criterion. The economic value of longevity can even be defined as the marginal economic benefit of a sow when she gets an extra parity. Pre-weaning survival can be chosen as a selection criterion for survival. Pre-weaning litter growth rate may be used as selection criteria for milk production. These three traits can be directly considered in a breeding program.

3.4.2. Indirect selection of robust pigs

Sensitivity to environmental variations is often measured by reaction norms. Knap (2005) proposed to compute an EBV for environment sensitivity through the slope of the regression of phenotype to environments. Several authors have used reaction norms to quantify the response to environmental variations (Knap and Su, 2008; Herrero-Medrano, 2015). This environmental sensitivity should be measured at the commercial level. Indeed, nucleus herds are highly protected environments, which largely differ from commercial herd environments. As a consequence, when their offspring are raised in a commercial herd, they do not express their full potential and may rank

differently than in the nucleus herd. Hence, EBV for level and slope of reaction norm for each trait between nucleus and production farm should be calculated then quantify robustness performance effects (Knap, 2005). Moreover, considering reaction norm model in estimating breeding values avoided confusion between GxE and additive genetic effect (Knap and Su, 2008).

3.5.Challenges to improve robustness

A large number of traits can be used to improve robustness. This may the case for health related traits or for immune response or the used genetic diversity because it helps animal to cope environment variability. Genomic selection is of high interest, because it allows us to select more robust pig on the basis of marker or gene information and to limit phenotyping to the reference population.

3.5.1. Selection for Immune response

Several authors (Wilkie and Mallard, 1999; Edfors-Lilja et al., 1993) have proposed to select less sensitive / more robust pigs based on immune response traits. They can be very numerous (e.g. Flori et al., 2011) and can be classified into categories, such as the innate vs the adaptive immune response, or humoral vs cell-mediated immune response. They proposed to use immune traits which are not pathogen-specific in order to try to cope with a large number of pathogens so as to improve robustness. This idea was also supported by Flori et al. (2011) who investigated the genetic variability of immunity traits in a Large White pig population. They showed that immune traits are genetically controlled, with moderate to high heritability. Wilkie and Mallard (1999) reported the main results of a selection experiment on an index combining several immune responses. They showed that the pig population selected for a higher immune response provided healthier and better growth performances over the other population.

3.5.2. Selection for adrenocortical axis responds

Selection for growth rate and carcass lean content has decreased cortisol production in French Large White pigs (Foury et al., 2009). Mormède and Terenina (2012) hypothesized that this lower cortisol production was responsible for a lower robustness and proposed a strategy to increase robustness by selecting pigs with a higher-level activity of adrenocortical axis. They showed in their review that the cortisol response to a stimulation of the adrenocortical axis had positive effects on functional traits and adaptation. Since plasma cortisol respond to ACTH was known as heritable (Larzul et al., 2015), a divergent selection experiment was set up in Large White pigs with lines

selected for either high or low cortisol response to an ACTH challenge (Larzul et al., 2014b). Results showed that the high adrenocortical axis activity (HAAA line had higher male reproductive performance, i.e. an increased semen concentration and total number of spermatozooids than the low line (LAAA). in the second generation, number born alive was higher in HAAA line than in LAAA. More recently, Bacou et al. (2016) provided evidence that the effect of an acute social stress in piglets was lower in HAAA line. However, HAAA also showed unfavorable trends for post-weaning growth. This experiment is ongoing and aims at getting a comprehensive role of cortisol as a tradeoff between productivity and robustness (Larzul et al., 2014b).

3.5.3. Taking advantages of genetic diversity

Genetic diversity is important because it helps animals to cope with current environmental variability, as well as to reduce the potentially deleterious effects of close relative breeding (Notter, 1999). Genetic diversity can be found between population and within population. Zhang et al. (2000) and Banville et al. (2015) discussed several strategies for taking advantage of prolific Chinese breeds as maternal components in crossbreeding schemes. Genetic variability within population should also be managed to avoid the increase in Inbreeding and to maintain genetic diversity (Notter, 1999; Colleau and Tribout , 2006; Delaunay and Merour, 2006). An intense selection within breed could increase inbreeding and decrease genetic variability. Genetic diversity is also the primary basis for adaption to future environmental uncertainty. The response to selection is depending on available genetic diversity in the population. But if not well planned, cross-breeding can fail to significantly improve productivity and lead to the loss of valuable characteristics such as the special ability to cope with extremes of temperature, limited water supplies, poor-quality feed, rough terrain, high altitudes and other challenging aspects of the production environment.

3.5.4. Genomic wide association studies on robustness traits

Genomic Selection is the selection of animals based on genomic markers. When the markers effects are known and it is known which markers the animal carries, the breeding value of the animal based on these markers can be calculated and can be used for selection (Calus et al., 2013). Genes are situated on the DNA and are responsible for the genetic differences between animals. For traits like milk production, hundreds of genes have an effect on the performance of an animal. It is unknown where exactly the genes that have an effect on specific traits are located and which variants of a gene (good or bad) the animal carries.

Table 3.1 . Implementation of genome wide association studies on robustness related traits

Authors	Methods	Traits interest	General conclusion
(Guo et al., 2016)	GWAS with linear mixed model and a Bayesian mixture model	Litter size and piglet mortality	This study detected QTL regions associated with litter size and piglet mortality traits in Danish pigs
(Mulder, 2016)	Simulation study	Environment sensitivity	Showed the benefit of norm reaction models and showed the benefit of genomic selection to exploit GxE compared to traditional sib or progeny testing schemes
(Sell-Kubiak et al., 2015)	GWAS and Double Hierarchical GLM	Litter size and their variability	Detected genomic regions associated with variability of total number born and can be used in genomic selection to decrease variability of TNB
(Serão et al., 2016)	GWAS and Bayes B method	Immunity and Reproductive data	results indicated a significant genomic component associated with PRRSV antibody response and number of stillborn
(Thekkoot et al., 2016)	GWAS and Bayes B method	Lactation performance	identified genomic regions associated with sow lactation feed intake and efficiency
(Lee et al., 2012)	Whole genome association analysis	Immunity	a total of 54 SNPs were detected associated with immunity traits

In table 3.1. Several genomic association studies have been used to select pig that could be related to robustness such as stillbirth, resistance to disease, sensitivity to environment and also longevity. Lower heritability of robustness related traits could be overcome by genomic selection. Genomic selection has been simulated in pig population (Cleveland and Hickey, 2013; Lillehammer et al., 2013; Tribout et al., 2013). Genomic selection can obtain a better exploitation of genetic variation within families that can produce a more accurate selection of candidates and a reduction of inbreeding in the investigated population (Sonesson et al., 2012) and it allows accurate estimation of breeding value for selection candidates that have no phenotypic records (Meuwissen et al., 2001).

4. Conclusion

This thesis showed that after 21 years of selection in French Large White Pig population have resulted in large improvements of sow numerical and weight productivity. However, this study provided evidence that these improvements have been accompanied by unfavorable effects of selection for several traits such as an increase in stillbirths and in post-natal mortality, a reduced longevity and productive life, a reduced milk production and robustness related traits such as an increased heterogeneity of performance from birth until slaughter. Based on the results of this study, modifying breeding goals in order to give more attention to robustness related traits should be considered.

This study also showed that frozen semen can be used to evaluate genetic trends in a selected pig population. Although it is a relatively late method to evaluate the effects of selection, it gives the opportunity to investigate a potentially unlimited number of traits. The use of frozen semen was able to measure genetic trends not only for productive and reproductive traits but also for a large number of new traits that were not routinely recorded. This has highlighted unexpected genetic trends and highlighted a number of traits that need to be carefully monitored in the context of the selection program. It may result in changes in the breeding goal of selected populations, as was the case in French dam populations with the replacement of total number born by number born alive or any other countries with the integration of longevity in the breeding goal. In other cases, the problem can be solved through management changes or combined breeding / management solutions.

A particular attention was given to trait variability and robustness, as several results tend to indicate that 'modern' pigs are less robust than 'older type' pigs. Robustness is a complex trait with different facets. Further research is needed to better understand its different components and to propose the most relevant selection methods for sustainable pig production.

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CURRICULUM VITAE

Parsaoran Silalahi was born on 20th of August, 1982, in Porsea, Indonesia. In June 2005, he graduated bachelor degree in Bogor Agricultural University (BAU). In his Bachelor report, he studied the effect of corn gluten feed as corn substitution in the rations on swine carcass quality and economic analysis". Then, In September 2008, he started a master degree in the same university and chose animal production and technology as specialization. During his master study, he got scholarship from Tanoto Foundation and OTORITA ASAHAN. In his master report he, studied the "Effects of sow feed addition with bangun - bangun plant meal (*Coleus amboinicus* Lour) on the performance of sow reproduction and piglets". Improving pig production through feed strategy did not interest him any longer, and then, in September 2012 he started a PhD degree (with scholarship from Directorate General Higher Education (DGHE), Education Ministry of Indonesia) in the same university, but in the Biology Reproduction Department. At that time, he assumed that he would finish his PhD in Indonesia. Fortunately, DGHE collaborated with French Embassy in Indonesia offered scholarship to perform the PhD in France. He started his PhD thesis in France in 2013 and worked on "Delta G" project at the Institut National de la Recherche Agronomique (INRA). The objective was to evaluate the effects of selection in French Large White pig population with a particular focus on traits related to sow reproduction and robustness. During his PhD thesis, he estimated the effects of selection on a large number of original traits and on trait variability, and found several undesired effects of selection suggesting a decreased robustness in LW population. During his PhD study, he also began to establish a scientific collaboration between INRA and BAU. In the middle of his stay in France, he and his supervisor were invited to present the PhD project and the PhD study results at an international conference in Indonesia. After this study, based on the results obtained within this thesis, he planned to go back to Indonesia, to set up breeding programs for pig production in Indonesia, which do not exist yet. The position as a young lecturer in BAU allows him to share and develop the scientific experience that he has obtained during his PhD period in France.

LIST OF PUBLICATIONS

Article 1- Silalahi, P., T. Tribout, A. Prunier, Y. Billon, J.-M. Gogu , and J.-P. Bidanel. 2016. Estimation of the effects of selection on French Large White Reproductive performance using frozen semen. *J. Anim. Sci.* 94:3655–3662.

Article 2- Silalahi, P., T. Tribout, J.-M. Gogu , Y. Billon, and J.-P. Bidanel. 2017a. Estimation of the effects of selection on French Large White sow and piglet performance during the suckling period. *J. Anim. Sci.* (Submitted).

Article 3- Silalahi, P., T. Tribout, A. Prunier, Y. Billon, J.-M. Gogu , and J. P. Bidanel. 2017b. Effects of selection and pre-weaning growth on the mean and variability of post-weaning growth and carcass performance of French Large White pigs. *Animal* (in preparation).

Article 4- Silalahi, P., T. Tribout, J.-M. Gogu , Y. Billon, and J.-P. Bidanel. 2017c. Selection changes the effects of sow features on growth and carcass performance of their progeny. *Asian-Australasian J. Anim. Sci.* (in preparation).

ORAL PRESENTATION IN A CONFERENCE

P. Silalahi, T. Tribout, J. Gogu , Y. Billon, J. P. Bidanel. 2015. Effects of selection on the efficiency of sow reproduction and maternal ability. In: 66th EAAP Annual meeting, Warsaw, Poland, 31 August – 4 September 2015.

P. Silalahi, T. Tribout, J. Gogu , Y. Billon, J. P. Bidanel. 2015. Effects of Selection on the Efficiency and Variability of Sow Reproduction and Maternal Abilities. In: 3rd International Seminar on Animal Industry, Bogor, Indonesia, 17-18 September 2015.

POSTER PRESENTATION IN A CONFERENCE

P. Silalahi, T. Tribout, J. Gogu , Y. Billon, D. D. Solihin, M. A. Setiadi, J.P. Bidanel. 2015. Evaluation des effets de la s lection sur l'efficacit  reproductive et la variabilit  des performances des truies. In : Journ es de la Recherche Porcine, 47, 47-48.

SEMINAR AND WORKSHOP

- 46 mes, 47 mes, 48 mes and 49 mes Journ es de la recherche porcine, Paris, France
- 17 me, 18 me and 19 me s minaire des th sards du d partement g n tique animale
- International Workshop RECOLAD, 11 and 12 February 2015 in Paris, France
- Autumn school on adaptive animal and livestock farming system to meet global change, 3 - 7 November 2014, agroCampusOuest, France
- 66th EAAP Annual meeting, Warsaw, Poland, 31 August – 4 September 2015.
- 3rd International Seminar on Animal Industry, Bogor, Indonesia, 17-18 September 2015

PROFESSIONAL SKILL SUPPORT COURSE

- Skills portfolio, 2013
- Building your base, 2014
- Poster power, 2014
- Write right, 2014
- Animal genetic, genome and diversity, 2014
- Introduction to R software, 2014

PhD students Discussion Group

- Accueil des nouveaux doctorants, 2013
- Journal club, 2014
- Journées ABIES, 2014, 2015 and 2016
- FRANCAIS LANGUE ETRANGERE, 2014, 2015 and 2016

Acknowledgments

This PhD degree would not be possible without the help and contribution of many people. I am very grateful to everybody that directly or indirectly contributed to the completing of this thesis.

I gratefully acknowledge the Directorate General of Human Resource for Science, Technology and Higher Education, Indonesia, Agreenium and INRA Animal Genetics Division for the financial support of the PhD thesis.

Thanks to my supervisor Jean-Pierre Bidanel, who provided me knowledge, confidence and friendship to finalize this PhD degree. Warm welcome and good discussion always left in my mind and encourage me to do more scientific work in my future career. It is much appreciated that you accept me as your student with a huge of patience. Clear direction during writing this thesis was very helpful for me and helped me to be more confident to do all steps to get this degree. We were student and supervisor at INRA, but we were also sometimes competitors or team members in soccer games.

To my supervisors in Indonesia, Prof Dr. Agus Setiadi and Dr. Dedy duryadi, Msc; with your recommendation in Bogor Agricultural University (BAU), I could continue my training in France. Good advices were motivating for me to spend more than three years in France. Thanks also to my colleagues in BAU for supporting me during my stay in France. Special thanks to Asnath, Hotnida, Yuni Cahya and Winarno.

Many thanks to committee members Catherine Larzul, Alban Bouquet, Laurienne Canario, Tatiana Zerjal, for sharing your knowledge. I would also say thanks to the members of GIS team, even we were localized in different buildings, but you always invited me to the meetings and the barbecue parties. Thanks also to the unforgettable PSGEN team who shared coffee every morning during these three years. I belong to this team by heart, I will remember all I have learned from you about life experience and advises how to take care of my little son. Many thanks for Denis Laloë, Tatiana, Andrea, Wendy, Agathe, Dominique, Eleonore and Xavier for “special wedding gift”. Thanks to all colleagues in GABI Unit that I cannot mention individually.

Since I arrived in France, Indonesia community ‘Bonapasogit Prancis’ and ‘Keluarga Catholic Indonesia’ became my second home and welcomed me as a family. Many things I have learned when we collaborated in all Indonesian activities and sharing experience and information how to life in France. It would have been hard to live without friends and community that could help me any time I needed. Special thanks to Christian LAMBLIN and Eric BROUSOULOUX and the family who received me and family to live together in warm home.

To my beloved wife, in last year of my study, I am lucky that you came to join me in France. You helped me to prepare everything before and after work. You always become the best for me, and also sometimes become my advisor to solve daily problems. Day by day, we pass with happiness and become unforgettable memories in our life. Now, Thomas Maruli Silalahi, our little handsome boy was born at the end of my PhD period to give more happiness in our family. I love you so much.

Titre : Evaluation expérimentale des effets de la sélection sur des caractères de reproduction et de robustesse dans une population de porcs Large White (en français)

Mots clés : semence congelée, évolution génétique, reproduction, robustesse, porc, croissance, survie des porcelets, poids à la naissance, performances de carcasse, variabilité des caractères, caractéristiques de la truie.

Résumé : Des progrès importants ont été obtenus dans les principales populations porcines pour les caractères inclus dans l'objectif de reproduction, à savoir la croissance, l'efficacité alimentaire, la composition de la carcasse et, dans les lignées maternelles, la prolificité des truies. Les animaux sélectionnés pour une forte efficacité productive peuvent être particulièrement sensibles à des problèmes comportementaux, physiologiques ou immunologiques, c'est-à-dire être moins robustes. Ces effets défavorables de la sélection sont souvent difficiles à mettre en évidence, car les caractères correspondants ne sont pas systématiquement enregistrés dans les programmes de sélection. L'utilisation d'un stock de sperme congelé est une méthode élégante pour estimer les évolutions génétiques pour un grand nombre de caractères (habituellement non enregistrés). Deux groupes expérimentaux (L77 et L98) ont été produits par

l'insémination de truies LW, nées en 1997-1998, soit avec du sperme congelé stocké à partir des verrats LW de 1977, soit avec du sperme frais de verrats nés en 1998. Cette étude a montré que deux décennies de sélection ont permis des progrès importants pour les principaux caractères d'intérêt, mais ont également affecté de façon défavorable des caractères tels que la longévité, le risque de mortalité, la variabilité de caractères, qui suggèrent un effet défavorable de la sélection sur la robustesse des porcs. Nos résultats soulignent la nécessité d'intégrer des caractères liés à la robustesse dans l'objectif de sélection des populations porcines. Il est donc nécessaire de poursuivre les recherches afin de mieux caractériser les différentes composantes de la robustesse et leur impact sur l'efficacité, le bien-être et la santé des porcs afin de pouvoir définir les objectifs de sélection les plus pertinents pour l'avenir.

Title: Experimental evaluation of the effects of selection on reproductive and robustness traits in a Large White pig population.

Keywords: frozen semen, genetic trend, reproduction, robustness, pig, genetic trend, piglet growth, piglet survival, birth weight, carcass performance, growth traits variability, sow features.

Abstract: Large improvements have been obtained in major pig populations for traits included in the breeding goal, i.e. growth, feed efficiency, carcass composition and, in maternal lines, sow prolificacy. Animals selected for high production efficiency may in particular be more sensitive to behavioral, physiological, or immunological problems, i.e., be less robust. These adverse effects of selection are often difficult to reveal, as corresponding traits are not routinely recorded in breeding programs. The use of stored frozen semen has been shown to be an elegant method to estimate genetic trends for a large number of (usually not recorded) traits. Two experimental groups (L77 and L98) were produced by inseminating French Large White (LW) sows born in 1997-1998 with either stored frozen semen from the

above-mentioned 1977 LW boars or with fresh semen from LW boars born in 1998. This study has shown that 2 decades of selection have resulted in large gains for major traits of interest, but have also adversely affected traits such as longevity, risk of mortality, trait variability, which tend to indicate an unfavorable effect of selection on pig robustness. Our results stress the necessity to integrate robustness related traits in the breeding goal of pig populations. Thus, further research is needed to better characterize the different components of robustness and their impact on pig efficiency, welfare and health to be able to define the most relevant breeding objectives for the future.