INFORMATION TO USERS

This manuscript has been reproduced from the microfilm master. UMI films the text directly from the original or copy submitted. Thus, some thesis and dissertation copies are in typewriter face, while others may be from any type of computer printer.

The quality of this reproduction is dependent upon the quality of the copy submitted. Broken or indistinct print, colored or poor quality illustrations and photographs, print bleedthrough, substandard margins, and improper alignment can adversely affect reproduction.

In the unlikely event that the author did not send UMI a complete manuscript and there are missing pages, these will be noted. Also, if unauthorized copyright material had to be removed, a note will indicate the deletion.

Oversize materials (e.g., maps, drawings, charts) are reproduced by sectioning the original, beginning at the upper left-hand corner and continuing from left to right in equal sections with small overlaps.

Photographs included in the original manuscript have been reproduced xerographically in this copy. Higher quality 6" x 9" black and white photographic prints are available for any photographs or illustrations appearing in this copy for an additional charge. Contact UMI directly to order.

Bell & Howell Information and Learning
300 North Zeeb Road, Ann Arbor, MI 48106-1346 USA
800-521-0600

DIRECT AND CORRELATED RESPONSES TO TWO-STAGE SELECTION FOR OVULATION RATE AND NUMBER OF FULLY FORMED PIGS AT BIRTH

By

Agustin Ruiz-Flores

A DISSERTATION

Presented to the faculty of

The Graduate College at the University of Nebraska

In Partial Fulfillment of Requirements

For the Degree of Doctor of Philosophy

Major: Animal Science

Under the supervision of Professor Rodger K. Johnson

Lincoln, Nebraska

August, 2000

Bell & Howell Information and Learning Company
300 North Zeeb Road
P.O. Box 1346
Ann Arbor, MI 48106-1346

DISSERTATION TITLE

Direct and Correlated Responses to Two-Stage Selection for Ovulation Rate and Number of Fully Formed Pigs at Birth

BY

Agustin Ruiz-Flores

SUPERVISORY COMMITTEE:

APPROVED	DATE
Rodger Johnson Signature Rodger K. Johnson Typed Name	2-17-00
Merlyn K Nielsen Signature Merlyn K. Nielsen Typed Name	2-17-00
Kreg A Leymaster Signature Kreg A. Leymaster Typed Name	2-17-00
Dale Van Vleck Signature L. Dale Van Vleck Typed Name	2-17-00
Walter W. Stroup Signature Walter W. Stroup Typed Name	2/17/00
Signature Typed Name	

GRADUATE COLLEGE
UNIVERSITY OF NEBRASKA

DIRECT AND CORRELATED RESPONSES TO TWO-STAGE SELECTION FOR OVULATION RATE AND NUMBER OF FULLY FORMED PIGS AT BIRTH

Agustín Ruíz-Flores, Ph. D.
University of Nebraska, 2000
Advisor: Rodger K. Johnson

The objectives were to quantify direct and correlated responses and to estimate genetic parameters for ovulation rate (OR), number of fully formed pigs at birth (FF), and other production traits following two-stage selection for OR and FF. Three lines were used. Line IOL was derived from a line previously selected eight generations for an index to increase OR and embryonic survival. The other two lines, COL and C, originated from line C_i, the control for the index line. Line IOL had greater OR (4.24±.38 ova) and FF (1.97±.39 pigs) at Generation 0 than lines COL and C. Lines IOL and COL underwent nine generations of two-stage selection. In Stage 1, all gilts from 50% of the litters with greatest FF were retained and OR were measured on them. Approximately 50% of these gilts were selected on OR in Stage 2. The gilts selected for OR were mated to boars selected from the upper one third of the litters for FF. The two-stage selection was repeated in their progeny. Line C was randomly selected. Each line had 35 to 55 litters by 13 to 18 sires per generation. Ovulation rate was measured by laparotomy 11 d after second estrus. The hypothesis was that selection for OR in a first stage, and on uterine capacity (UC) in a second stage cam increase litter size. An animal model including,

depending on the trait, the random additive direct, additive maternal, and common litter of birth effects and fixed effects of generation and sex was used. At Generation 9, differences in mean EBV for OR and FF between lines IOL and C were 6.20±.29 ova and 4.66±.38 pigs; differences between lines COL and C were 2.26±.29 ova and 2.79±.39 pigs; and differences between lines IOL and COL were 3.94±.26 ova and 1.86±.39 pigs. Coefficients for regression of line mean EBV on generation number were .27±.07 ova/generation (P<.01) for OR, and .35±.06 pigs/generation (P<.01) for FF in line IOL; .30±.06 ova/generation (P<.01) for OR, and .29±.05 pigs/generation (P<.01) for FF in line COL; and .01±.07 ova/generation (P>.10) for OR, and .02±.05 pigs/generation (P>.10) for FF in line C. The two-stage selection procedure was effective in improving both OR and FF. All the increase in OR was realized as an increase in FF in line COL. Number of fully formed pigs at birth increased more than OR in line IOL presumably because UC was limiting litter size at generation 0 in this line. Correlated responses to selection for OR and FF were decreased age at puberty and increased prenatal loss and birth weight. Inconsistent correlated responses were found for growth and backfat in the two lines selected. Two-stage selection seems to be a promising procedure to improve litter size in swine.

ACKNOWLEDGEMENTS

I would like to thank my major advisor Dr. Rodger K. Johnson for his encouragement, guidance, patience, and dedication to the best interest of my Ph. D. program. I am also indebted to my supervisory committee members Dr. Merlin K. Nielsen, Dr. Kreg A. Leymaster, Dr. L. Dale Van Vleck and Dr. Walter W. Stroup for their valuable suggestions regarding my graduate and research programs.

I also want to thank everybody in the Department of Animal Science and especially to faculty and students of Breeding and Genetics for their friendship, assistance and sympathy. This research program could not have been possible without the daily work of the Swine Research Station staff at Mead, NE. To all of them thanks so much.

I wish to extend sincere thanks to the Consejo Nacional de Ciencia y Tecnología (México), Fundación García Robles-Fulbright-Institute of International Education, Banco de México and University of Chapingo, especially my colleagues of Breeding and Genetics of the Department of Zootecnia, for allowing the time and for providing financial support during my Ph. D. program.

DEDICATION

This dissertation is dedicated to my parents and my family. I especially acknowledge the unconditional support from my family. I thank my wife María Ofelia, my son Gustavo, and my daughter Roxana for their support, unselfishness, and immense patience during my Ph. D. program. I could not have achieved this goal without their love. I extend my dedication to the Martínez-Ruíz and Alonso families and to my nephew Israel, those moments we spent together are unforgettable. Also I want to express my appreciation to our friends Cuauhtemoc Cervantes Martínez, Rodolfo Ramírez Valverde and family, and the Pelayo, Rowe, Sahai, Mua, Surjawan, Tsuruta and Pratt families.

Table of Contents

List of Tables

CHAPTER I. Literature Review

CHAPTER II. Direct and correlated responses to two-stage selection for ovulation rate and number of fully formed pigs at birth

List of Figures

Chapter I. Literature review

Introduction

The economic importance of reproductive traits, specifically litter size, is well documented in the literature (Mitchell et al., 1982; Tess et al., 1983; Smith et al., 1983; De Vries, 1989). Increases in expected overall economic responses by adding litter size to an index for growth and carcass traits varied from 2 to 5% and from 10 to 18% for general purpose and maternal lines, respectively (Avalos and Smith, 1987). In addition, with the genetic progress attained by the pork industry for growth and performance traits the importance of reproductive traits will be increased more (Haley et al., 1988; Haley and Lee, 1992).

Litter size is the main component of productive efficiency of the sow (Bidanel et al., 1994). The need to select for components of litter size is reinforced by the fact that genetic improvement of litter size is difficult (Haley et al., 1988), unless high selection intensities are applied to large populations (Legault and Gruand, 1976). Several selection criteria to increase litter size in pigs have been used. In early work it was demonstrated that ovulation rate, one of the components of litter size, responds to selection (Zimmerman and Cunningham, 1975; Cunningham et al., 1979). Results from research aimed to improve components of litter size have been successful (Johnson et al., 1984; Bennett and Leymaster, 1989, 1990a, 1990b). Johnson et al. (1984) developed an index combining ovulation rate and embryonic survival to maximize expected increase in litter size. Experimental results agreed well with theoretical expectations (Johnson et al. 1999).

Among gilts chosen for ovulation rate, the number of fully formed pigs at birth is expected to measure uterine capacity as selected gilts are expected to have ovulation rate that exceeds uterine capacity. An experiment to test this hypothesis was conducted at the research station of the University of Nebraska at Mead, NE. This experiment was to test the hypothesis that selection with emphasis on ovulation rate in a first stage and uterine capacity in a second stage will result in an increase in litter size. The objectives of this study were to use data from the experiment: a) to estimate genetic and phenotypic parameters for ovulation rate, number of fully formed pigs at birth, and other production traits, and b) to quantify direct and correlated responses for these traits resulting from two-stage selection.

I. Physiology of pregnancy in the sow

Pregnancy is a dynamic process of interrelationships between fetuses and uterus. The establishment of pregnancy is probably the most critical phase. Most of the prenatal mortality occurs in this phase.

1. 1. Establishment of pregnancy

Fertilization occurs in the oviduct, at the ampullary-isthmic junction, subsequent to mating and approximately 3 to 8 h after ovulation (Stroband and Van der Lende, 1990). Embryos are particularly sensitive to changes in progesterone level at critical stages of early pregnancy (Wilmut et al., 1990).

In the pig, establishment of pregnancy begins about 11 to 12 d from estrus (Roberts et al., 1993). Embryos synthesize and release estrogens during this period. Estrogens participate in the maternal recognition of pregnancy in the sow. Although conceptus estrogen synthesis triggers a number of uterine secretory events on d 11, a second sustained phase of estrogen stimulation from d 14 to 18 appears to be necessary for luteal maintenance beyond 25 d. Also, the conceptus secretes a number of biologically active substances such as catechol estrogens, prostaglandins and polypeptides, which interact with estrogen to prevent luteolysis (Geisert et al., 1990).

Establishment and maintenance of pregnancy not only include the conceptus block to luteolysis, but also involve conceptus-endometrial interactions to control vascular permeability, blood flow, placental attachment and immunological protection. Uterine arterial blood flow increases with increased estrogen levels (Geisert et al., 1990;

Roberts et al., 1993). In this way the conceptus can maintain the locally elevated flows for its survival (Ford and Stice, 1985).

Changes in the timing and magnitude of progesterone concentration affect the uterine environment, which affects embryo viability. Progesterone is believed to play a major role in controlling maternal secretion of nutrients, growth factors and enzymes required for successful embryo development (Groothuis et al., 1997). The maintenance of adequate progesterone levels by ensuring that luteolysis mechanisms are overcome or suppressed is an essential function of the relationship between the conceptus and the endometrium. Also, progesterone stimulates endometrial retinol-binding protein secretion (Adams et al., 1981). This protein participates in the transportation of nutrients to the embryo-fetus.

Prostaglandin $F_{2\alpha}$ ($PGF_{2\alpha}$) is known for its luteolytic actions in corpora lutea. In contrast, the role of prostaglandin E_2 (PGE_2) in corpus luteum has received limited attention. Intrauterine infusion of PGE_2 lengthens the lifespan of corpora lutea (Akinlosotu et al., 1986) and intraluteal administration or intrauterine infusion (Akinlosotu et al., 1988) of PGE_2 prevents luteolysis induced by PGF_2. In addition, PGE_2 stimulates progesterone production by luteal cells from gilts by day 12 of the estruous cycle and during early pregnancy (Wiesak et al., 1992). Therefore, PGE_2 is often considered luteotrophic and important in the function of the corpus luteum during the establishment of pregnancy.

1. 2. Embryonic development

The union of sperm and egg pronuclei during the syngamy process forms the zygote. The embryos are retained within the oviduct for 2 d. Eventually, rising progesterone levels seem to cause dilatation of the oviduct and, as a result, transport of embryos to the uterus occurs (Dziuk, 1985). The zygote cleaves when passing down from the oviduct to the uterus at the 4 to 8 cell stage 2 to 3 d after ovulation (Dziuk, 1985; Noden and De Lahunta, 1985; Stroband and Van der Lende, 1990). Pig embryos remain at the tip of the uterine horn until about day 6 when they migrate to the uterine body. By day 9, some embryos are in the opposite horn from where they were released. Migration continues until day 12. After day 12, embryos can no longer successfully move (Dziuk, 1985). Estrogens seem to play an important role during migration. Migration seems to be the result of myometrial activity due to estrogen stimulation.

Cleavage results in the formation of a cluster of cells called morula. Cell division continues through the 16 to 32 cell stage morula to formation of the blastula at about 5 to 9 d post-fertilization (Hughes et al., 1996). During the blastocyst stage the embryo increases in size at a rate from 30 to 45 mm up to 1 cm per h. The blastocyst stage in the pig is reached at days 5 to 6 and the cell number at the moment of blastocyst formation is usually 16 to 32 (Stroband and Van der Lende, 1990). Hatching from the zona pellucida occurs at days 6 to 7. The hatching process is probably independent of cell number because hatched blastocysts varying from 80 to 135 cells have been found (Stroband and Van der Lende, 1990). The diameter of the newly hatched blastocyst is approximately .2 mm (Geisert et al., 1982b).

Pig trophoblast cells consume their yolk shortly after hatching, indicating increased metabolism and a growing dependency on uterine substances. The zona pellucida no longer prevents certain molecules from reaching the trophoblast. Experiments using ferritin or peroxidase have shown that pig trophoblast cells easily absorb these macromolecules by means of pinocytosis (Stroband et al., 1984). From 11 to 12 d, pig blastocysts begin to elongate and to be reduced in diameter, resulting in filamentous structures up to 100-cm long. Elongation is not uniform in all conceptuses due to variation in stages of development.

Cellular differentiation occurs in the blastocyst (Noden and De Lahunta, 1985; Stroband and Van der Lende, 1990). The larger cells form the embryonic disk. The cells on the periphery of the blastocyst are trophoblast cells. Their role is to facilitate the absorption of nutrients in early embryonic development and later to participate in the formation of extra-embryonic membranes, which contribute to the formation of the placenta. Embryos attach to the uterine wall approximately 12 to 13 d after fertilization. Placentation is complete around 24 d of gestation. Approximately 75% of blastocysts present on day 9 of pregnancy survive to complete placentation (Pope and First, 1985). Embryos are spaced nearly equidistant from each other. The position of the fetuses in the uterus affects the spacing between fetuses. Fetuses at the tip of the horn before day 25 have the greatest space with the space decreasing from the tip to the body of the horn. Due to resorptions near the body of the horn, the space per live fetus is greater and roughly equal near the body and the tip after day 35. Fetuses in the middle of the horn are

most likely to have limited space and be smaller at birth than their litter mates (Dziuk, 1985).

Prenatal mortality varies from 17% (Dyck, 1974) to 46% (Marrable and Ashdown, 1967). Most embryonic loss occurs in the first 40 d of gestation (Flint et al., 1982; Pope and First, 1985; Bazer et al., 1988). High prenatal mortality often is associated with high ovulation rates (Wrathall, 1971). Competition for endometrial secretions (histotrophe) has been proposed to be a major cause of embryonic loss (Bazer, 1975). The influence of sow nutrition on this factor is receiving increased attention (Zak et al., 1997; Quesnel et al., 1998; Mao et al., 1999). Asynchrony between embryonic development and uterine environment has also been proposed as a major factor in embryo loss (Pope and First, 1985; Pope et al., 1990; Roberts et al., 1993).

Zak et al. (1997) and Quesnel et al. (1998) reported an inhibitory effect of short-term, severe feed restriction on pulsatile LH secretion in lactating sows. Mao et al. (1999) did not find improvement in reproductive performance after weaning in primiparous sows restricted-fed after 21 d of lactation by using exogenous GnRH treatment.

1. 3. Uterine morphological changes

The uterine wall consists of the serosa, the myometrium and the endometrium. The wall is folded in such a way that opposite folds interlock and reduce the lumen space. Alterations in the uterine ultrastructure of embryonic germ layers and cytological changes in uterine epithelial cells suggest a close relationship between embryonic and uterine development in early pregnancy (Stroband and Van der Lende, 1990).

The uterine environment affects the developmental competence of the blastocyst. At the time of maternal recognition of pregnancy, developmental variation exists in the blastocysts (Pope et al., 1986; 1990). This variation in developmental stage originates from differential follicular maturation (Hunter and Wiesak, 1990). Pope et al. (1986, 1990) hypothesized that more advanced embryos initiate changes in the uterine environment, which are detrimental to the less developed embryos. The more advanced embryos, by synthesizing more estradiol, advance uterine secretions. The lesser developed embryos probably become more susceptible to this new environment and eventually die in an asynchronous environment.

Estrogens and progesterone modulate the synthesis and secretion of uterine proteins after day 5 (Simmen et al., 1988). Around day 11, embryonic signals lead to the abrupt release of the vesicles (Geisert et al., 1982a). The low survival rate after transfer of pig embryos cultured for up to 27 h compared to embryos transferred immediately shows that the loss of viability in vitro may occur rapidly (Davies, 1985). This result indicates the importance of the uterine environment.

With respect to macro morphological changes, Wu et al. (1988a) reported a linear increase in weight and diameter ($P<.01$) in gravid uteri between 15 and 27 d of gestation. Increases in length, weight, and diameter of uterine horns began by day 18, but not before. On the other hand, Pope and First (1985) reported that the uterus lengthens early in the luteal phase relative to the edematous length at estrus. However, no significant elongation occurs from day 7 to 12. Elongation appears to occur as a result of two

mechanisms, an early endocrine induction and a later lengthening due, perhaps, to distension as fetal fluids accumulate.

Breed differences in uterine morphological changes exist. Biensen et al. (1998; 1999) hypothesized that the lack of increase in placental size in Meishan sows during late gestation is one of the key differences resulting in increased litter size exhibited by Meishan compared with U.S. and European pig breeds. They used the ratio of fetal to placental weight as an index of placental efficiency. This ratio determines in a comparative way, the number of grams of fetus that a gram of placenta is supporting during late gestation. These authors suggested that litter size could be increased by selecting offspring with a greater than average placental efficiency. Between day 90 and term, Meishan fetal growth depends on progressive increases in placental blood vessel density and requires no increase in placental size. In contrast, Yorkshire conceptuses seem to rely exclusively on placental-endometrial surface area for nutrient exchange (Biensen et al., 1998).

II. Direct selection for litter size

Heritability of litter size is about .10 in swine (Bichard and David, 1985; Haley et al., 1988), rabbits (Blasco et al., 1993b), and mice (Kochera-Kirby and Nielsen, 1993). The number of experiments regarding direct selection on litter size in swine is limited. In addition to swine, and due to their short generation interval, low cost, and relatively easy management, researchers have used mice (Bradford, 1968; Falconer, 1960, 1971; Joakimsen and Baker, 1977), and rabbits (Blasco et al., 1993a, 1993b, 1994; Bolet et al.,