# Deviation of the Secondary Sex Ratio after Natural Mating or Artificial Insemination in the Domestic Pig: The Influence of the Sex Composition of the Breeding Population 

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#### Abstract

Sex ratio plays an important role in livestock production, with female animals often being favoured over males. To achieve the deviation towards the desired sex, breeding practise exclusively uses biotechnological methods aimed at manipulating the sex ratio of the offspring of farm animals, with sexed semen being the most widely used technique. However, there are also several biological mechanisms involved in offspring sex ratio deviation that could potentially be used in livestock production, such as local mate competition (LMC) or local resource competition (LRC). In wild mammal populations, competition for mates and resources is normally relaxed by dispersal, but not in domestic mammals, which normally live under specific (farm) conditions - unnatural sex composition of the group, no spontaneous dispersal of offspring due to captivity. One could therefore assume that local competition operates in the domestic mammal population. Accordingly, the aim of this short communication was to address the possible function of a type of (quasi)-LMC/LRC in domestic pigs under farm conditions and its possible influence on the secondary sex ratio of the offspring. Here the sex ratio of 1484 piglets, 1041 from artificial insemination (sires from allmale population, no female presence) and 443 from natural mating (sires from strongly female population composition), with all mothers from strongly female population composition, was studied. The sex ratio of piglets from artificial insemination was balanced ( $1: 1 ; \mathrm{X}^{2}=0.05, \mathrm{p} \geq 0.05$ ), while the offspring from natural mating were significantly male-biased ( $\mathrm{x}^{2}=4.99, \mathrm{p}<0.05$ ). No clear relationship was found between sex ratio and litter size, parity or season. Although there are some limitations to the interpretation of the results presented here, it appears that the highly skewed sex composition of the population to which the breeding males/females belong may result in a more competitive mating environment, causing the sex ratio of the offspring to deviate towards the other sex, which is otherwise dominant in the population. This phenomenon of sex allocation in domestic mammals could be a tool in animal husbandry to manipulate (even if only slightly) the sex composition of the offspring of domestic mammals.


Keywords: domestic pig, sex ratio, sex allocation, local competition

## INTRODUCTION

In his theoretical model of equal investment, Fisher (1930) explained that natural selection favours equal parental investment in both sexes, but only in the complete absence of environmental influences (for details see West, 2009). Under natural conditions, however, several environmental factors play a role in sex allocation. First, interactions between relatives should be taken into account. For example, Hamilton (1967) showed that populations in which the sons of a female are likely to compete mainly with their brothers for
mating opportunities (i.e., in which populations are highly structured and males do not disperse) should have offspring sex ratios that are more biased towards females than in populations in which unrelated males compete for mates. This situation is termed Local Mate Competition (LMC). However, LMC appears to be just a specific form of Local Resource Competition (LRC) first described by Clark (1978), who showed that sex ratios can be skewed in favour of either sex for a variety of reasons. For example, when daughters and mothers compete for resources (food, space), the sex ratio may be biased in favour of males. Competition for resources/
mates is relaxed by dispersal (Dobson, 1982), and predicts a sex ratio that favours the dispersing sex.

Furthermore, Trivers and Willard (1973) have described the opposite situation, termed Local Resources Enhancement (LRE), in which the overproduction of one sex has an enhancing effect on the fitness of its relatives, e.g. in cooperatively breeding species. They also suggested an adjustment of the sex ratio in the offspring in response to environmental conditions. When environmental conditions are good (e.g. abundant food), investment is shifted in favour of the sex that derives the greater fitness advantage from being produced under better/optimal environmental conditions, and vice versa (i.e. the Trivers-Willard hypothesis). Thus, in polygynous species (such as the pig), investment in female offspring has the greatest evolutionary benefit when food is scarce, while males raised in suboptimal conditions are unlikely to compete with other males for mates as adults.

Most research derived from the Trivers-Willard hypothesis (Trivers and Willard, 1973), which makes explicit predictions based on the individual. But as mentioned already, the characteristics of the (local) population to which a reproducing individual belongs have a significant influence (West et al., 2002; Booksmythe et al., 2017), e.g. population density, LMC, LRC.

The influence of population density on sex ratio has been previously confirmed in mammals (Kruuk et al., 1999; Wells and Van Vuren, 2017), including LRC (Cockburn et al., 1985; Hewison and Gaillard, 1996; Landete-Castillejos et al., 2001). LMC, on the other hand, has been extensively tested and confirmed almost exclusively in insects (especially wasps). In mammals, LMC (also referred to as the population sex ratio hypothesis) has been tested but not confirmed, e.g. in the grey-tailed vole (Bond et al., 2003).

Furthermore, a facultative context-dependent adjustment of the offspring sex ratio in response to a given level of LMC/LRC is to be expected in systems with regularly fluctuating levels of such competition. In other words, facultative adjustment is favoured to exploit a temporary difference between the sexes in competition for resources/mates. A related idea is that when generations overlap, the expected reproductive value of sons and daughters depends on the sex ratio of the population. In this case, it is more profitable to produce sons when the sex ratio of the population is fe-male-biased than when it is male-biased since the expected reproductive outcome "per son" is higher in a female-biased population.

We derived our hypothesis from a somewhat unconventional interpretation of LMC/LRC, which predicts a skewed sex ratio for offspring due to local competition between mates in a same-sex pig population under farm conditions with little or no dispersal. We therefore hypothesised that breeding individuals living in a population with a highly skewed sex composition tend to shift the offspring sex ratio
towards the other sex, which is otherwise dominant in the population.

## MATERIALS AND METHODS

Data on the secondary sex ratio (the ratio of males to females at birth) of domestic pigs were collected for the period from 2001 to 2016 by the Pig Research Centre of the Faculty of Agriculture and Life Sciences at the University of Maribor. Approval from the University Ethics Committee was not required.

The sex ratio of 136 litters (1484 piglets) of different parental breeds/crossbreeds (Slovenian Landrace; Large White; Pietrain; Duroc; Krškopolje pig; and Hybrids 12 and 54) was included in the analyses: 41 litters ( $\mathrm{n}=443$ ) arose from natural insemination/mating ( N ) and the rest from artificial insemination (A). The average litter size was $10.85 \pm 3.61$ for A and $11.00 \pm 2.53$ for N . The samples/litters were comparably distributed over the seasons. The individual sows and boars were randomly and evenly represented in the sample.

All sows included in the analyses were exposed to the same environmental conditions (housing and feeding regime) and lived in the same high-density structured population. Overall, 1) the herd consisted primarily of breeding females and their offspring, 2) there was always only one intact boar present in the herd of $30-40$ sows and he had constant contact with sows in oestrus, 3) the females had no contact with other males except male conspecifics in the first weeks of life, but which were surgically castrated in the first days after birth, 4) two thirds of the fertile females were artificially inseminated (with a total of 37 different boars from an external population in the indicated period), and the rest were naturally mated (with a total of 9 different boars in the indicated period). Boars used for natural mating were not used for artificial insemination and vice versa. The use of all boars was optimised according to standard procedures, avoiding overuse but maintaining consistency (normally 1 ejaculate/week for young boars and up to 3 ejaculates per week for older boars, with an appropriate recovery period after use).

Sows were artificially inseminated with semen processed according to the standard procedure (diluted with extender and divided into several doses). The semen was provided by an (external) insemination station where the males lived in a male-only population.

Statistical analysis was carried out using the SPSS statistical package. The frequency of male and female offspring was determined for artificial and natural insemination. Deviation from the expected sex ratio (1:1) was tested using the chi-square test. The sex ratio (number of males/number of females) was calculated in general and per litter. According to the sex ratio of the litter, five groups were formed (< 0.5 , $0.5-1.0,1.0-1.5,1.5-2.0,>2.0$ ) and the distribution among these
groups was compared between artificial and natural insemination. In addition, the frequencies of males and females in relation to litter size ( $\leq 9,10-12, \geq 13$ ), parity ( $\leq 2,3-5, \geq 6$ ) and season (winter, Dec.-Feb.; spring, Mar.-May; summer, Jun.Aug.; and autumn, Sept.-Nov.) were compared and tested with the chi-square test.

## CASE RESULTS

Of 1041 artificially conceived piglets from 95 litters, 524 were males and 517 females. The overall ratio did not deviate from 1:1. In contrast with artificial insemination, sex ratio of offspring sired by natural mating indicated statistically significant male-biased sex ratio, with $55.3 \%$ male and $44.7 \%$ female offspring (Table 1).

A more detailed analysis showed different patterns of sex ratio (male/female) in natural and artificial insemination. Figure 1 shows the percentage of litters with a particular sex ratio. The highest percentage of litters ( $\sim 39 \%$ ) in natural and artificial insemination had a sex ratio between 0.5 and 1.0 , with no differences between insemination methods. On the other hand, the two surrounding classes (sex ratio < 0.5 and $1.0-1.5)$ showed the most marked differences. In the lowest class (sex ratio < 0.5 ) there were only $2.5 \%$ naturally inseminated litters, while over $21 \%$ of litters were artificially inseminated. In the third class $(1.0-1.5)$ the ratio was exactly the opposite with $27 \%$ naturally inseminated litters and only $9.5 \%$ artificially inseminated litters.

The results on the relationship between litter size and parity on sex ratio showed no clear patterns (Table 2), with a significant ( p < 0.05) male bias in small litters conceived naturally, but the same pattern in medium sized artificially inseminated litters. The sex ratio in relation to parity did not deviate from 1:1 in any case, but showed a tendency towards a male-biased ratio only in naturally inseminated sows from parity 6 (Table 2). Finally, the sex ratio showed


Figure 1: Distribution of naturally and artificially inseminated litters into sex ratio classes ( $\mathrm{X}^{2}=12.70, \mathrm{p}=0.0128$ )
neither significance nor a tendency in relation to the season (data not shown).

## DISCUSSION

In the present study, we found that in a strongly femalebiased population (where only one whole boar was present at a time), naturally mated animals living in it tended to produce male-biased offspring. Furthermore, in the same female-biased population an even sex ratio (1:1) was found when females were inseminated by boars living in an external all-male population in the insemination station. According to these results, we could conclude that the sex ratio depends mainly on the boar involved in reproduction, but this contradicts numerous studies conducted in mammals showing a strong female influence on offspring sex ratio (Charnov, 1982; West, 2009; Douhard, 2018). Therefore, caution is needed in interpretation, as also shown by previous studies on sex ratio in domestic pigs, which do not give a clear answer, but whose results and interpretations are rather controversial (Meikle et al., 1997; Mendl et al., 1997; Soede et al., 2000; Alfonso, 2005; Kennedy and Moxley, 2010; Zindove et al., 2021).

Alfonso (2005), for example, reported on the sex ratio of four different farms/populations that did not show clear patterns in terms of sex ratio and type of insemination, with a significantly female-biased sex ratio in the case of artificial insemination with external males, while the other population under the same reproductive conditions showed an unbiased sex ratio, which was also the case in the population with combined insemination (artificial, natural) with external males. In addition, Alfonso (2005) reported a significantly male-biased sex ratio in the population artificially inseminated with boars from the same population, which is also consistent with the study by Baxter et al. (2012). In these studies, however, the sex composition of the population in which the reproducing animals lived was largely unknown (not reported), but as we shall see here, population structure should be given special consideration.

First of all, in wild boar, males are dispersing sex. Considering LRC, domestic pigs therefore hold the capacity of a higher (commonly referred to as maternal) investment in male offspring, which have a higher reproductive potential (Fernández-Llario et al., 1999). But if dispersion is constrained in any way, the competition is expected to operate. Consistent with the LMC/LRC (both described in the introduction) and the assumption that both females and males participate in sex ratio adjustment, the following premises can be derived, which are supported by the results presented here: 1) breeding animals, either females (sows) or males (boars), from extremely female-biased populations with high densities without adequate dispersion strive to produce male-biased offspring, 2) conversely, breeding animals from
extremely male-biased populations with high densities without adequate dispersal strive to produce female-biased offspring, and 3) when animals from a population with an extremely lopsided sex composition breed with animals from a population with an extremely opposite sex composition, their influences are expected to be neutralised and they produce sex-balanced offspring (1m:1f).

Both pre- and postnatal manipulation of sex ratios has mostly been attributed to the influence of the mother, and thus studied mainly from this perspective, while the paternal role has been essentially neglected (see the discussion in Douhard, 2018). However, the role of the male (that is, of both parents) in the sex allocation of the offspring does not appear to be negligible at all (James, 1996; Malo et al., 2017; Lavoie et al., 2019). In addition to our results, this thesis was also supported in the study on pygmy hippopotamus,
which showed a skewed ratio of X and Y chromosome-bearing spermatozoa in the ejaculate (Saragusty et al., 2012), with a clearly female (X) biased spermatozoa ratio. Yet, in the pygmy hippopotamus, a female-biased sex ratio was observed in both parents, suggesting that females are the dispersing sex and that parents may reduce competition for local resources (LRC) by producing more females. Considering a possible $\mathrm{X} / \mathrm{Y}$ bias in semen, semen from boars living in an all-male population (in our case artificial insemination) is expected to be female, i.e. X-biased, and contrary, Y-biased semen is expected to be produced in males living in an all-female population (in our case natural mating).

Besides population composition, the other factors examined in the present study, i.e. season, litter size and parity, showed a slight but no clear pattern/relationship with the sex ratio deviations, which incidentally is consistent

Table 1: Frequency of male and female piglets produced either by artificial insemination (sows from the female-biased composition of the population and boars from the male-biased population) or by natural mating (mothers and boars from the female-biased composition of the population)

| Inseminations method | n | Male (\%) | Female (\%) | Sex ratio $^{1}$ | $X^{2}$ | p |
| :--- | :---: | :---: | :---: | :---: | :---: | :---: |
| Artificial | 1041 | 50.3 | 49.7 | 1.01 | 0.05 | n.s. |
| Natural | 443 | 55.3 | 44.7 | 1.24 | 4.99 | $*$ |
| Total | 1484 | 51.8 | 48.2 | 1.08 | 1.96 | n.s. |

* p <0.05; ${ }^{1}$ males/females

Table 2: Frequency of male and female piglets produced either by artificial insemination (sows from the female-biased composition of the population and boars from the male-biased population) or by natural mating (mothers and boars from the female-biased composition of the population) in relation to the litter size and parity

|  |  | n | Male (\%) | Female (\%) | Sex ratio ${ }^{1}$ | $\chi^{2}$ | p |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| Litter size |  |  |  |  |  |  |  |
| Small ( $\leq 9$ ) | Artificial | 192 | 50.0 | 50.0 | 1.00 | 0.00 | n.s. |
|  | Natural | 102 | 60.8 | 39.2 | 1.55 | 4.26 | * |
| Medium (10-12) | Artificial | 390 | 56.2 | 43.8 | 1.28 | 4.88 | * |
|  | Natural | 161 | 53.4 | 46.6 | 1.15 | 0.41 | n.s. |
| Large ( $\geq 13$ ) | Artificial | 459 | 45.5 | 54.5 | 0.83 | 3.66 | $\dagger$ |
|  | Natural | 180 | 53.9 | 46.1 | 1.17 | 1.09 | n.s. |
| Parity |  |  |  |  |  |  |  |
| Low ( $\leq 2$ ) | Artificial | 415 | 48.4 | 51.6 | 0.94 | 0.41 | n.s. |
|  | Natural | 88 | 54.5 | 45.5 | 1.20 | 0.73 | n.s. |
| Medium (3-5) | Artificial | 322 | 48.8 | 51.2 | 0.95 | 0.20 | n.s. |
|  | Natural | 218 | 55.0 | 45.0 | 1.22 | 2.22 | n.s. |
| High ( $\geq 6$ ) | Artificial | 304 | 54.6 | 45.4 | 1.20 | 2.58 | n.s. |
|  | Natural | 110 | 59.1 | 40.9 | 1.44 | 3.64 | $\dagger$ |

[^0]with previous findings in the domestic pig (Clutton-Brock and Iason, 1986; Soede et al., 2000; Alfonso, 2005; Zindove et al., 2021). In addition, other possible factors, such as heat stress, coital rate, etc., could play a role in sex ratio bias (Saragusty et al., 2012). Further, it can be said that semen from artificial insemination is processed with extenders, homogenised, etc., and thus any potential for (natural) sex ratio adjustment may be lost, and the processing of the semen could also affect the viability of X- or Y-bearing spermatozoa.

However, we were not able to test all factors potentially related to sex allocation using the data we obtained. Furthermore, we did not have data on the timing of insemination or the duration of semen storage that could hypothetically influence the sex ratio due to the different survival of $\mathrm{X} / \mathrm{Y}$-bearing spermatozoa (in general, X is more resistant); however, the studies on the timing of insemination did not show convincing results (e.g. Rorie, 1999; Soede et al., 2000; Martinez et al., 2004), while the duration of sperm storage showed some influence on the sex ratio (Olsson et al., 2007; Park et al., 2021). Finally, breeding individuals might also contribute differently to the overall sex ratio. Yet, the sample size did not allow us to test for possible individu-al-level effects.

Although many factors influencing sex ratio in mammals are already known, the mechanisms behind them are not yet fully understood. However, several explanations have already been proposed, pointing to context-dependent effects either on gametes (spermatogenesis, spermatozoa viability/survival, sperm motility, etc.) or on the course of embryonic development (Krackow, 1995a; Cameron, 2004). At the embryonic level, sex ratio deviations have further been explained by sex-dependent asynchrony between early embryonic development (slowly developing female versus rapidly developing male blastocysts) and uterine responsiveness to implantation (Krackow, 1995b; Krackow, 1997; Krackow and Burgoyne, 1998). In addition, plasma glucose has been found to influence early embryonic development, with higher concentrations promoting male conceptus development but inhibiting female conceptus growth and development (Cameron, 2004; Cameron, 2008).

Indeed, sex ratio in general is crucially influenced by conditional fluctuations in the production and secretion of gonadotropins (FSH, LH) and reproductive (and even stress) steroid hormones (oestrogen/oestradiol, testosterone, progesterone, cortisol) in parents of both sexes around conception or in early embryonic development (e.g. Krackow, 1995a; Krackow, 1997; Creel et al., 1998; James, 1996; Cameron, 2004; James, 2008).

Although the results presented here should be viewed and interpreted with some caution, as the data were collected "ad hoc" and not based on an experimental design, the resulting sex ratio could be explained in the context of
local environmental conditions/population structure (LMC/ LRC) manifested by parental influence on the sex ratio of offspring in domestic pigs, thus providing a potential tool for manipulating sex ratio in domestic mammals.

It appears that the sex composition of the population to which the breeding animal belongs (either female or male) should not be ignored in the context of sex allocation in domestic mammals. Apart from its potential application value, knowledge of the biological mechanisms behind sex allocation is also important in mammalian breeding, where females are often preferred. Because females require more time and resources for reproduction than males, while a high number of fertile females in the population is necessary to ensure efficient (methodical) reproduction and selection.

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# Odstopanje sekundarnega spolnega razmerja po naravnem pripustu ali umetni osemenitvi pri domačem prašiču: Vpliv spolne strukture plemenske populacije 

## IZVLEČEK

Razmerje med spoloma igra pomembno vlogo v živinoreji, pri čemer so samice pogosto preferirane pred samci. Za doseganje želenega spola se v rejski praksi uporabljajo izključno biotehnološke metode, namenjene manipulaciji razmerja med spoloma potomcev rejnih živali, pri čemer je najbolj razširjena tehnika uporaba seksiranega semena. Vendar pa obstaja tudi več bioloških mehanizmov, vključenih v odstopanje razmerja med spoloma potomcev, ki bi se lahko potencialno uporabili v živinoreji. Med te sodi na primer lokalna konkurenca za spolne partnerje (ang. »Local Mate Comeptition«, LMC) ali lokalna konkurenca za vire (ang. »Local Resource Competition«, LRC). V populacijah divjih sesalcev se konkurenca za spolne partnerje in vire običajno sprosti z disperzijo osebkov, ne pa tudi pri domačih sesalcih, ki običajno živijo v specifičnih (farmskih) razmerah - nenaravna spolna struktura populacije, brez spontane disperzije potomcev zaradi ujetništva. Domnevamo torej lahko, da v populaciji domačih sesalcev vlada visoka lokalna konkurenca. V skladu s tem je bil cilj tega kratkega prispevka, preučiti potencialno delovanje (kvazi-)LMC/LRC pri domačih prašičih v farmskih pogojih in potencialen vpliv na sekundarno razmerje med spoloma potomcev. V raziskavi je bilo proučeno razmerje med spoloma za 1484 pujskov, od tega 1041 osebkov, ki so izšli iz umetne osemenitve (merjasec iz populacije, ki je v celoti sestavljena iz samcev, brez prisotnosti samic) in 443 iz naravnega pripusta (merjasec iz populacije, v kateri so močno prevladovale samice). Vse matere so izhajale iz populacije s prevladujočo žensko sestavo. Razmerje med spoloma pri pujskih pri umetni osemenitve je bilo uravnoteženo ( $1: 1 ; \chi^{2}=0,05, p \geq 0,05$ ), medtem ko je bilo razmerje pri potomcih iz naravnega pripusta značilno odklonjeno v prid samcev ( $\mathrm{x}^{2}=4,99, \mathrm{p}<0,05$ ). Rezultati niso pokazali jasne povezave med razmerjem spolov ter velikostjo gnezda, zaporedno prasitvijo ali sezono. Čeprav obstajajo nekatere omejitve pri razlagi dobljenih rezultatov, se zdi, da lahko izrazito enospolna sestava populacije, ki ji pripadajo osebki vključeni v reprodukcijo, povzroči odklone razmerja med spoloma potomcev, t.j. odstopanje proti nasprotnemu spolu, ki sicer prevladuje v populaciji. Ta pojav odstopanja spolnega razmerja pri domačih sesalcih bi lahko v živinoreji uporabili kot orodje za manipulacijo (čeprav le rahlo) spolne strukture potomcev domačih sesalcev.

Ključne besede: domači prašič, spolno razmerje, spolna dodelitev, lokalna konkurenca


[^0]:    $\dagger 0.05 \leq \mathrm{p}>0.10$; * $\mathrm{p}<0.05$; ${ }^{1} \mathrm{males} /$ females

