Chapter 3

Behavioral Factors Affecting Reproduction in Domestic Horses: Sociobiological Approach

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Additional information is available at the end of the chapter

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Abstract

Fetal loss is a common phenomenon in domestic horses, being usually highest (up to 40%) of all domestic ungulates. However, in all studies investigating this problem, sociobiological approach, such as conflict between the evolutionary interests of individuals of the two sexes, has been neglected. Here we summarize results of three consecutive studies considering infanticide as a male's reproductive strategy and a mare's counter strategies against it. When a mare was either artificially inseminated or removed from her home environment and transported elsewhere for mating and then returned back into her home environment, containing a stallion (and/or gelding) who did not sire her fetus, she got into a potentially infanticidal danger. She more likely disrupted her pregnancy than a mare living in an environment with the sire of her fetus. This was highly affected by the social environment. Lowest percentage of pregnancy disruption can be achieved when the pregnant mare was released into an enclosure shared with the non-sire male whom she can "convince" he is the father of her expected foal by promiscuous mating. The effects of social environment leading to pregnancy block and/or disruption may thus explain substantial part of the high incidence of domestic horse fetal loss.

Keywords: pregnancy disruption, domestic horse, Bruce effect

1. Introduction

Fetal loss is a common phenomenon in domestic horses, being usually substantially higher than that in other domestic ungulates such as cattle (3.62–6.9%) [1, 2], goats (13%) and sheep (7.5%) [3]. Among Sable Island feral horses, fetal loss, as deduced from fecal oestrogens, reached up to 37.3% [4]. Even in young healthy domestic horse mares, approximately 10%

of detected pregnancies were lost during the first 5 weeks of gestation, while, in older mares, many embryos died before the first pregnancy check [5].

There have been a number of studies which have sought to explain an unusually high incidence of fetal loss in domestic horses reaching up to 40% [4–14]. However, these studies, as well as many breeders and veterinarians, neglect other factors associated with reproductive fitness and female reproductive strategies across species [e. g., [15]] One of those neglected factors may be sexual conflict, a conflict between the evolutionary interests of individuals of the two sexes [16], broadly investigated in behavioral ecology and sociobiology [15]. This conflict, originally driven by natural selection, might be further altered by physical and social environment in breeding practise.

2. Infanticide

While there are miscellaneous ways of sexual conflict one of the forms of interest in context of early fetal loss is infanticide (i.e. killing of conspecific's offspring by the individuals of the same species) by males, which causes serious costs on female reproductive success [17]. According to the original sexual selection hypothesis infanticide improves male mating success by accelerating the return of females to fertilizable condition [18, 19]. In seasonal breeders the benefits of infanticide by males is in improvement of the female breeding condition [18, 20–22]. The study of red deer (*Cervus elaphus*) was the first to provide empirical support for this hypothesis [22], which has been invoked for other mammals [18]. Many authors reviewed the possible female counterstrategies to infanticide ranging from polyandrous mating [17, 18, 23–25], through pregnancy block [26–29], later called "Bruce effect" [30–33], up to individual behavior such as maternal aggression, association with coalitionary defenders of either sex, etc. [18].

2.1. Infanticide in equids

The incidence and forms of infanticide varies among numerous mammalian groups. Sociality and social organization are among the most important predictors determining infanticide [34, 35]. The variability of incidence of male infanticide among various species and even subspecies was also reported specifically in equids [36, 37]. Based on interspecific differences in social organization, male infanticide has been suggested advantageous in all equid species, such as plains zebra, *Equus burchelli*, with exception of asses, *E. africanus*, *E. hemionus*, and *E. kiang* or Grévy's zebra, *E. grevyi* [37, 38].

In line with this prediction, the male infanticides was reported in Przewalski horse, *Equus przewalskii* [39–43], mountain zebra, *Equus zebra* [44, 45], plains zebra *Equus quagga* [36, 45], and domestic horse *Equus ferus caballus* [46–48]. Equids thus represent the group of ungulates with highest reported incidence of male infanticide.

In a herd of Przewalski's horses Feh and Munkhtuya [43] investigated male's infanticide and found that infanticide did not reduce birth intervals which they interpreted as contradictory to sexual selection hypothesis. Instead they concluded that male's infanticide is either linked to crowding or to human disturbance. Nevertheless, they did not consider any other potential benefits of premature termination of lactation by male's infanticide such as improving the female condition and thus her future reproductive success as suggested by others earlier [18, 20–22] and which has been proposed also for equids [39, 49]. Horse mares commonly become pregnant within a month or less after parturition of the previous foal [e. g., [50–52]]. They are thus sensitive to intensive maternal investment due to concurrent pregnancy and lactation. Pregnant mares cope with parallel investment into a nursed foal and a fetus through enhancing nursing behavior in early stages of pregnancy before the initially low requirements of the fetus increase [53]. Nevertheless, lowering mare's investment for costly nursing allocated to non-filial offspring by killing it may significantly advance resources invested in stallion's own progeny.

Hoesli et al. [39] suggested an additional alternative benefit of killing a dependent foal for the new-coming stallion. This might be the elevated testosterone level in a newly established harem stallion and the reluctance of mares to accept a new breeding partner. Altogether, male's infanticide in equids should be thus taken into consideration.

Our investigation to the present chapter has not been straight-forwarded. In context of those days knowledge, initially we investigated the possibility of forced copulation as an alternative to infanticide in the plains zebra. At that time, feral domestic horse mares were found to foal in alternate years or in two out of three years [54]. Killing a lactating offspring could improve the dam's condition increasing her chance to conceive within the same season. This resembled similar situation and reasoning for existence of infanticide as a male's reproductive strategy in a seasonal breeder, in red deer [22]. Foeticide as an extension to infanticide has also been reported as a candidate for improving reproductive success of a male in feral horses [55] as well as for captive plains zebra [36, 45]. Generally speaking invading males could induce abortions in females as a result of forced copulations [55] or just sexual harassment [56] and these aborting females would be then inseminated by the new males. Though, abortion subsequent to forced copulation has not been reported in numerous other feral populations of domestic horse [54, 57]. Although still interpreted as a possible forced copulation, our data on captive zebras did not show either any convincing evidence that the forced copulation by a new-coming stallion was the actual cause of abortion. What we did found, however, was that the probability of foal death was greatest when the new male joined the herd just after conception and decreased with increasing time between conception and date of the new male introduction - the chance of a foal surviving was less than 5% just after conception and more than 50% at the time of delivery [45]. The loss of pregnancy in the zebra mares after a new non-sire male joined the herd [36, 45] made us to testing the presumption that the "Bruce effect" could explain fetal loss in domestic horses [48]. It is presumed that the logic of the "Bruce effect" as a female counter-strategy to infanticide is to prevent the waste of energy in producing offspring likely to be lost [17, 18, 23, 58].

It is a common practice that the domestic horse mare is removed from her home environment and transported elsewhere for mating. After conceiving she is returned back into her home environment and social group, containing often familiar stallions and geldings [48]. If we presume that the behavioral adaptation for infanticide relevant for wild or free-ranging horses has not be lost in domestication, and it is obvious that it remained at least within feral populations [46, 47], then we may expect that, unless prevented by fencing or other management measures, the dominant males in the home social group may subsequently attempt infanticide.

3. Reproduction failure in domestic horse mares

We have investigated the problem in three subsequent reports where we described detailed methods and statistical analysis [48, 59, 60] and hence we will avoid presenting these details here. Basic tested hypothesis was that if the domestic horse mare was removed from her home environment and transported elsewhere for mating and then returned back into her home environment, containing a stallion (and/or gelding) who is not sire of her fetus, she would be more likely to disrupt her pregnancy than a mare living in an environment with the sire of her fetus. After conceiving she is returned back into her home environment and social group, containing often familiar stallions and geldings. This basic hypothesis was tested in the first study [48]. In the second step we investigated if a mare may consider pregnancy caused by artificial insemination as a pregnancy induced by a strange stallion [59], and finally we elucidated what happens when an out of home mated mare returns into male-free environment [60].

The reproductive data analyzed in the three steps originated from a questionnaire (**Table 1**) on reproduction of individual mares distributed subsequently to private horse owners in the Czech Republic. As the conditions under which the mares could contact (at least visual or vocal) home males differed among facilities, we used the term “enclosure” for any fenced area in which the horses were kept, regardless of the presence or absence of grass.

3.1. Reproduction failure after mating mares out of home and bringing them back to an environment containing a stallion and/or gelding

We obtained data for mares kept with one or more stallions and/or geldings present, either in the same or adjacent enclosure or further separated from the mares. All mares involved were positive in pregnancy testing after the mating and/or artificial insemination and before transportation home, which is a common routine in the country. The tests are usually performed between 2 weeks and 120 days after presumed conception [48].

In total 81 records of 60 different mares aged from 4 to 24 years, giving birth to 0 to 5 foals, and bred between years 1994 and 2008 were collected. The mares belonged to 21 breeds and came from 30 individual breeders. In 20% of cases artificial insemination was used. The age and previously successful pregnancies of the mares were (mean ± s. e. m.) 13.00 ± 0.92 years and 1.94 ± 0.32 foals for the mares mated with a home stallion and 12.46 ± 0.72 years and 1.99 ± 0.25 foals for those mated with a foreign stallion [48].

Of those mares mated with a foreign stallion outside the home stable, 31% aborted. In contrast, none of the 36 mares who conceived with a home stallion disrupted pregnancy (**Figure 1**). Five of the mares experienced both situations in different pregnancies, to be mated with a home stallion (n = 6, one mare was mated in two different seasons) and with a foreign stallion (n = 5).

Characteristic
Information on the mare:
Year of her birth
Breed *
Number of foals she had delivered
If she was nursing a foal when pregnant (Yes/No)
If she was transported during her pregnancy (Yes/No)
If she was transported during her pregnancy, then how many times
Number of failing pregnancies before the analyzed one
Type of use (Breeding/Racing/Sport/Recreational riding/Draught/Other)
Housing (Stalls/Loose boxes/Group housed in a barn/Group housed in paddocks/Pasture)
How was the mare kept on a pasture and/or in a paddock (Alone/In a group/Not at all)
Time (hours) spent daily on a pasture and/or in a paddock
Year of mating/insemination
Month of mating/insemination
How many times mated or inseminated
Transported elsewhere for mating/insemination (Yes/No)
Method of breeding (Pasture or paddock mating/In-hand breeding/Artificial insemination)
Immobilization of the mare during mating (None/On a leading rope/Lifted forelimb/Hindlimb hobbles/Twitch/Other)
Time spent with a stallion in free-running mating (days)
Date of parturition
Number of horses kept within the facility regardless of the housing system
Number of adult mares kept within the facility regardless of the housing system
Number of adult home stallions kept within the facility regardless of the housing system
Number of adult home geldings kept within the facility regardless of the housing system
Where were the adult mares kept within the facility* (Same enclosure as the pregnant mare/ out of the enclosure)
Where were the adult home stallions kept (Same enclosure as the pregnant mare/ out of the enclosure) **
Where were the adult home geldings kept (Same enclosure as the pregnant mare/ out of the enclosure) **
Conditions under which the mare was kept elsewhere if transported for mating out of her home stall:
How many days did the mare spent out of her home stall
If the mare was tested for pregnancy before returning home (Yes/No)
Number of foreign adult stallions kept within the facility where the mare was staying for mating and/or insemination
Number of foreign adult geldings kept within the facility where the mare was staying for mating and/or insemination
Where were the adult mares kept (Same enclosure as the pregnant mare/ out of the enclosure) **

Characteristic
Where were the foreign adult stallions kept (Same enclosure as the pregnant mare/ out of the enclosure) **
Where were the foreign adult geldings kept (Same enclosure as the pregnant mare/ out of the enclosure) **

*Akhal-Teke, American quarter horse, Arabian, Austrian warm-blooded horse, Belgian draft horse, Czech saddle ponies, Czech warm-blooded horse, Friesian, Furioso, Haflinger, Hanoverian, Hutsul horse, Lipizzaner, Old Kladruby horse, Purebred Spanish horse, Saxon, Silesian cold-blooded horse, Thoroughbred, Welsh cob, Welsh pony, cross-breeds.

**Detailed description where the other animals were kept was available. This included in an adjacent box, in a distant box, within the same enclosure as the mare or in the adjacent enclosure. Since this did not appear significant, the details are omitted in the table.

Table 1. Questionnaire on reproduction of the mares involved and conditions under which the mares were living during the analyzed pregnancy.

Also, in this case, none of the mares conceiving with home stallion disrupted pregnancy. On the other hand, 3 of the 5 mares (60%) conceiving with a foreign stallion aborted. Over one half (53.33%) of the mares who conceived with a home stallion were transported during their pregnancy, most of them repeatedly. None of the transported mares mated with home stallion aborted [48].

We fitted the statistical model for the mares that were transported to another facility for mating with a foreign stallion, and then returned to their home stable containing home stallion or gelding (PROC GENMOD, SAS version 9.1, designed for repeated measurements). The probability of pregnancy disruption depended on two effects only: whether the mare subsequently shared the home enclosure with at least one stallion and/or gelding (**Figure 1**) and on the number of foals the mare had delivered in the past (**Figure 2**). Pregnancy disruption was much more likely when the mare had no male company in her enclosure but one or more home stallions or geldings in adjacent enclosure were present, than when stallions and/or geldings were sharing the same enclosure with the mare (**Figure 1**, odds ratio = 6.99). With an increase in the number of foals delivered the probability for the mare to abort decreased (**Figure 2**).

Some respondents to our questionnaire reported increased sexual activity by a home stallion or dominant gelding shortly after the mare returned from mating with a foreign stallion if released into the enclosure with them. In 78.13% of cases mating of the pregnant mare by home stallion and/or gelding sharing the same enclosure was reported.

We have thus shown that in domestic horses, bringing a pregnant mare into proximity with a male who was not the father of her fetus increases probability of pregnancy disruption. In contrast to earlier studies on equids [36, 45, 55] and in agreement with Kirkpatrick and Turner [57], we suggested that forced copulations were unlikely to cause fetal loss in this study, since more losses were reported where home males were in adjoining enclosures than when they were in the same enclosure as the pregnant female. Pregnancy disruption was 7 times more likely when the mare had no male company in her enclosure but one or more home stallions or geldings were in an adjacent enclosure [48].

As reviewed by Becker and Hurst [31], "pregnancy disruption in rodents is triggered by semiochemicals in urine, most likely oestrogens [61, 62], that are pumped into the vomeronasal organ

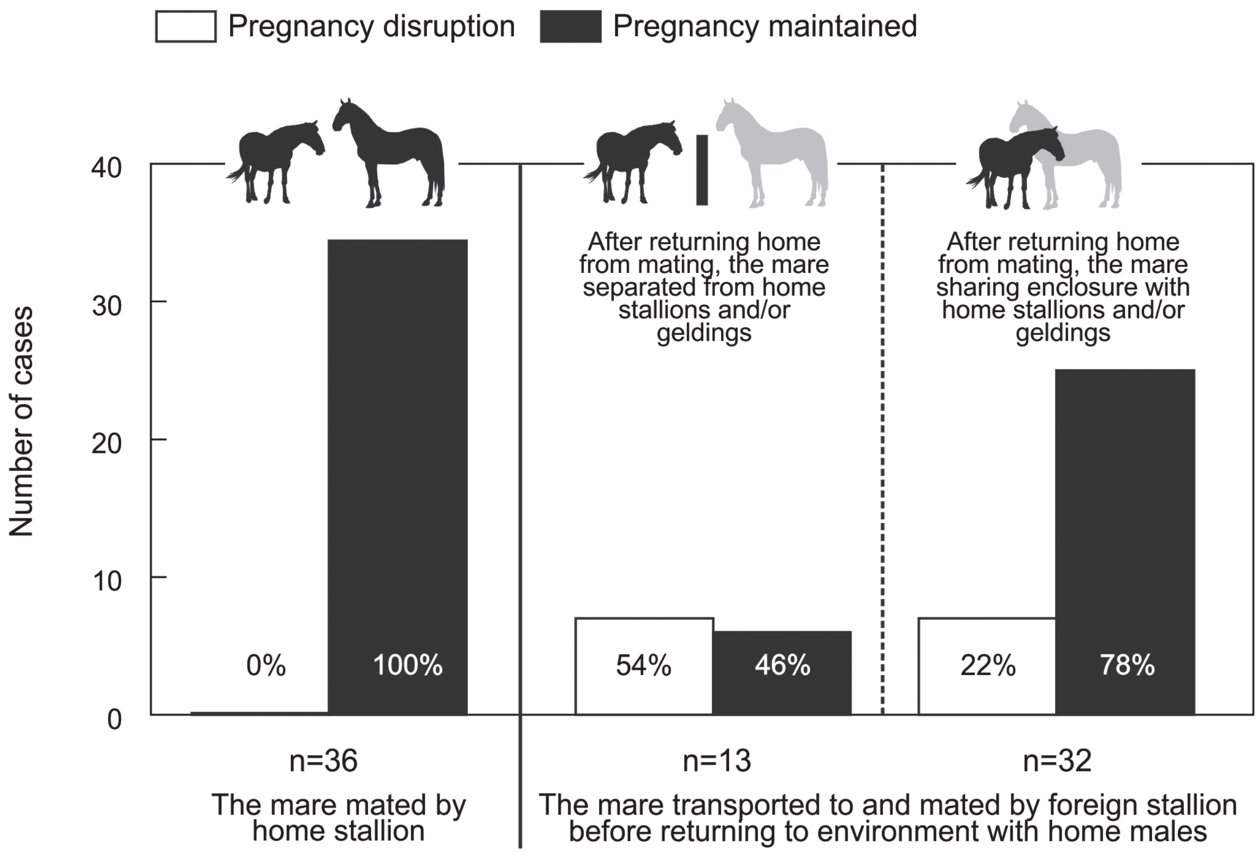

Figure 1. Proportion of pregnancy disruption in mares mated either by a home stallion or transported to and mated by a foreign stallion before they returned to environment containing home males (stallions and/or geldings) which were either separated from the returned mare or shared enclosure with her (reprinted from [48], permission for reuse provided by Springer nature).

following nasal contact with male scent. This activates a specific vomeronasal neuroendocrine pathway that inhibits prolactin release causing luteolysis and hence pregnancy failure. It was unlikely for the mares to contact with urine of the males located on the other side of the fence and to avoid possible effect of urine of the males within the same enclosure. Therefore, we can only speculate there is some other mechanism than the classical Bruce effect leading to luteolysis and hence pregnancy block in the mare" [48].

Pregnant mares in our study have been seen to be sexually active at times when conception was impossible in line with many other studies [63–68]. Such a sexual behavior can be interpreted as to confuse paternity [24, 30]. The males that had copulated with a given female are generally inhibited from killing young for the time period in which their offspring would be vulnerable to infanticide [17, 69]. Multi-male mating by females confuses paternity, thereby deterring infanticide by males. Such multiple mating is relatively common in mammals, occurring in over 100 species [25]. In many of these species, females also engage in nonprocreative mating [70]. Pregnant mares in our study isolated from home males by a fence were seen standing close to the neighboring male behind the fence, frequently urinating and soliciting him [48]. The same type of behavior was reported in rodents, primates, carnivores, and insectivores as a counter-strategy against male's infanticide [25].

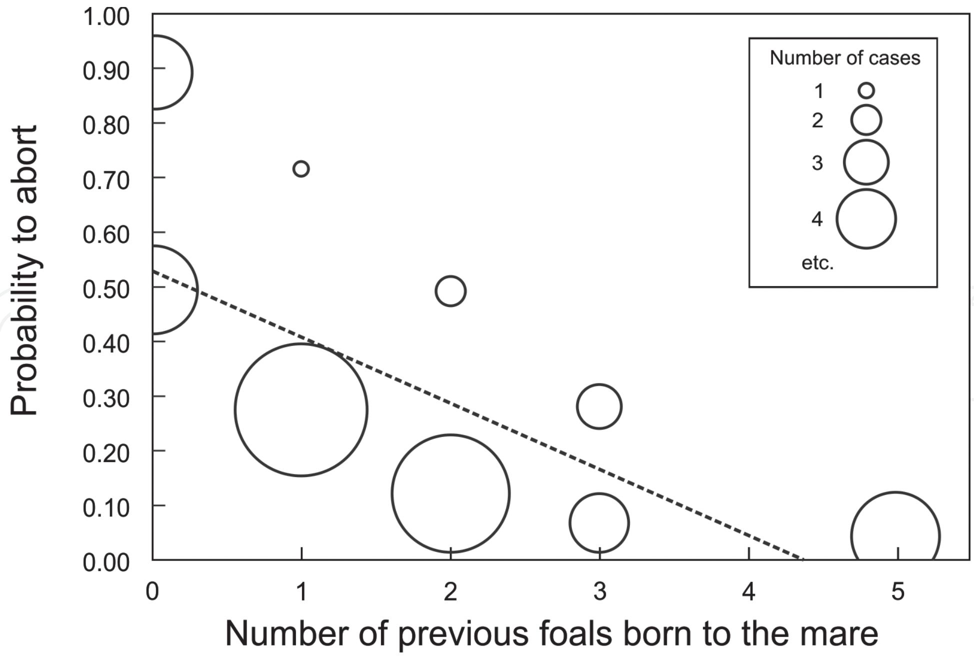

Figure 2. Predicted probability to abort by domestic mares plotted against the number of foals delivered in the past (reprinted from [48], permission for reuse provided by Springer nature).

We concluded that increased abortion among mares who had no direct access to home males (different enclosures) was as a direct result of a lack of opportunity in such situations to confuse home males about parentage. Termination of pregnancy in this way may thus be seen as an adaptation to save energy and avoid likely future infanticidal loss of their progeny.

We interpreted our results so that where possible, an out of home mated pregnant mare by behaving promiscuously she manipulates the home male's paternity assessment. If she has no chance to do that she may abort the current fetus. We cannot explain the mechanism yet, but speculate that this may be a mechanism actually activated by the mare [48].

3.2. The role of artificial insemination in pregnancy disruption

Artificial insemination (AI) is becoming increasingly used for initiation of pregnancy in domestic horses [71–73]; it was thus of interest to enquire whether disruption of pregnancies induced by AI occurs as frequently as after mating with a strange stallion away from home, and is affected by the same factors in the home social environment. Although an effect of natural versus artificial insemination was checked in the dataset analyzed in the first study, where it was found non-significant [48], a small proportion of AI in all pregnancies could affect the non-significant result. Therefore, we have collected more convincing amount of data for the next analysis.

Using PROC GLIMMIX for binary distribution (SAS version 9.4 with the mare's identity as a random effect), we analyzed 77 records of 51 different mares after AI, aged from 3 to 20 years,

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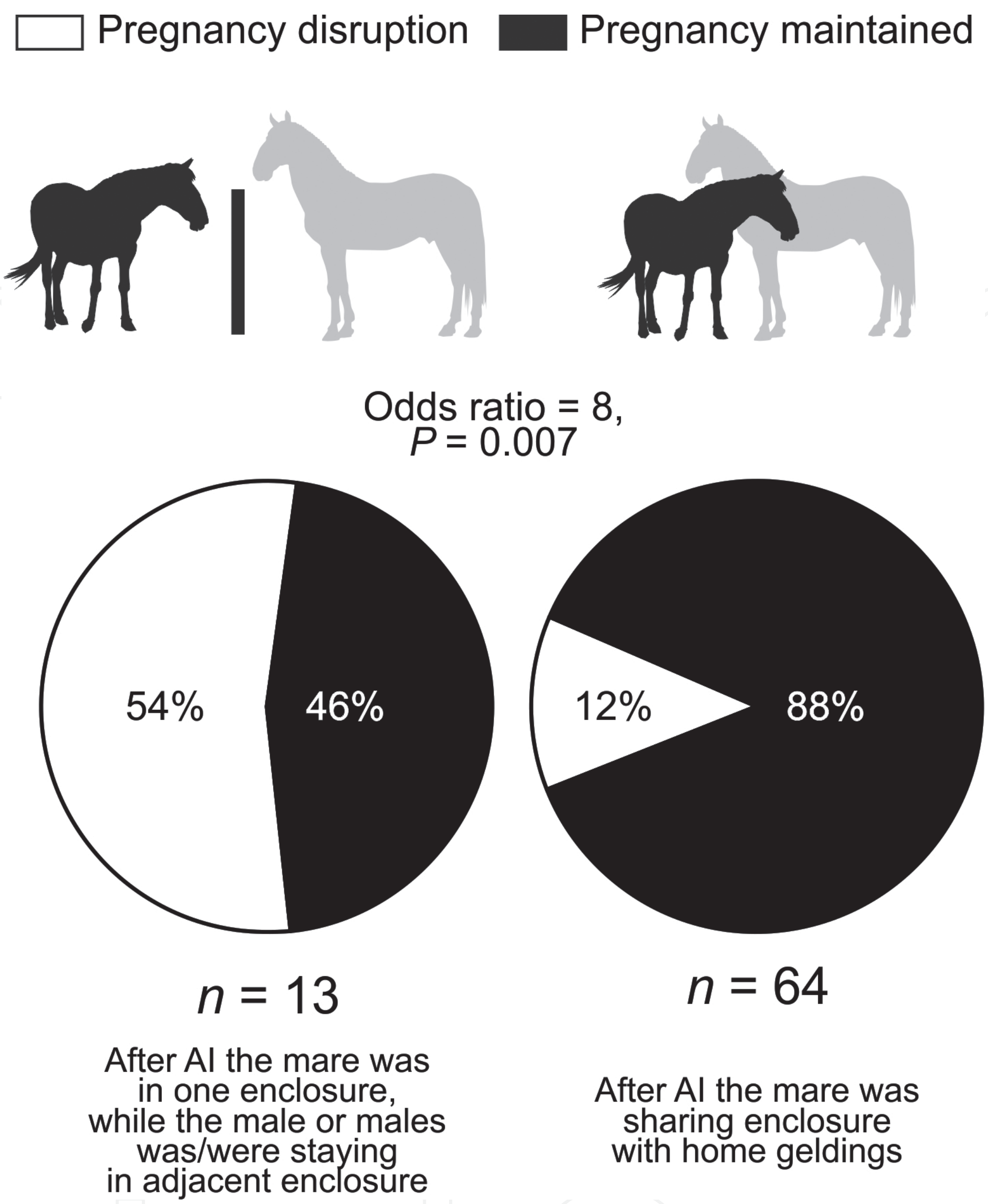

Figure 3. Proportion of pregnancy disruption according to social environment after AI of the mare according to social environment of the mare (reprinted from [59], permission for reuse provided by Oxford University Press).

giving birth between 0 and 13 foals, and bred between years 1984 and 2011. They belonged to 19 breeds and came from 21 individual breeders. As in the previous study [48], the probability of pregnancy disruption after AI depended on two effects only: social environment in which the mare was maintained after insemination (**Figure 3**) and the number of foals the mare had delivered in the past (**Figure 4**). As for natural mating the probability of failing reproduction was 8 times (odds ratio) more likely when the mare had no male company in her enclosure whereas stallions or geldings were present in an adjacent enclosure than when the mare was sharing the enclosure with geldings (in no case the mare was sharing the enclosure with a stallion). The results suggested that pregnancy disruption may equally be stimulated by the

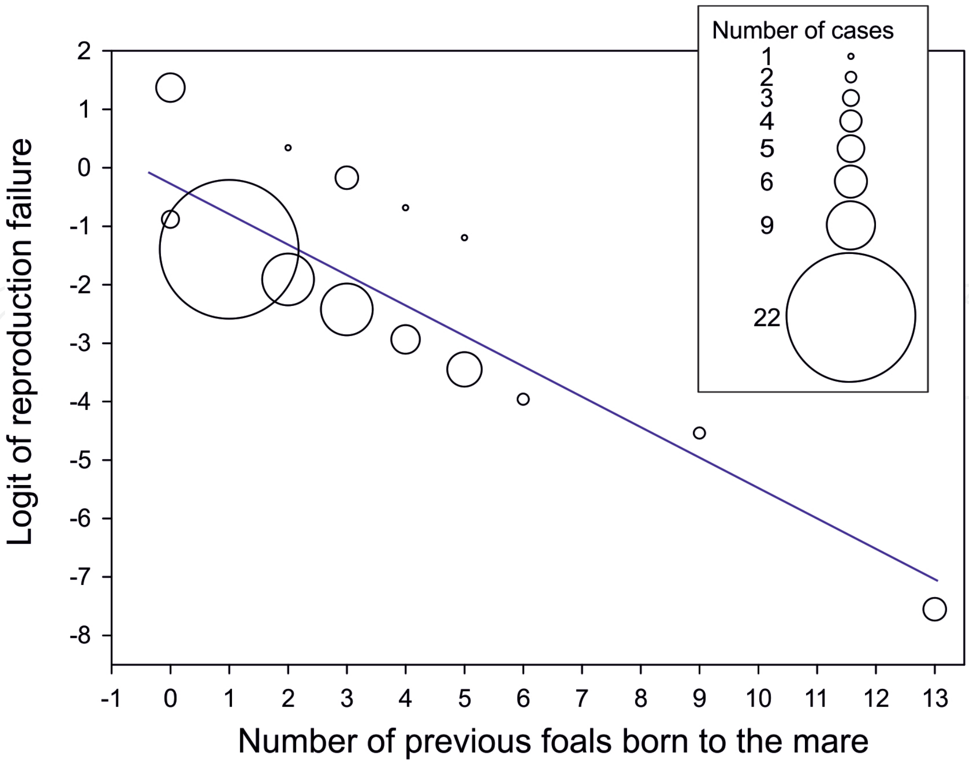

Figure 4. Probability of pregnancy disruption plotted against the number of previous foals born to the mare (reprinted from [59], permission for reuse provided by Oxford University Press).

social circumstances of the home environment in mares inseminated artificially as in mares mated naturally away from home. Present data thus support the prediction that the mare perceives conception after AI equally as mating with a new stallion.

3.3. The role of male free environment in pregnancy disruption

Since we published the results of the two above studies [48, 59], one additional questions had arisen. We did not consider the outcome if the pregnant mare was brought back to home farm containing mares only. Hence, in the final study on the domestic horse we tested the hypothesis that an incidence of a pregnancy disruption induced by a pregnant mare will be higher in a situation when a pregnant mare is in potential danger of the male's infanticide, compared to the situation when a pregnant mare is not in such a danger and/or can manipulate the male's paternity assessment by promiscuous mating [60].

For testing the hypothesis we used all the away-mated females from the previous study [48], extended them with additional 31 new records from pregnant mares mated away and then returned back to their home environment with one or more stallions and/or geldings ("home males"), and 34 records including situations with mares mated away and brought home to environment surrounded only by females herd mates. As in the initial study, all mares involved were positive in pregnancy testing carried out after mating. In total, there were 110 records of 75

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different mares aged from 3 to 20 years, giving birth between 0 and 13 foals, and bred between years 1984 and 2011. They belonged to 21 breeds and came from 37 individual breeders [60].

Also in this last study on the domestic horse the data were analyzed with the aid of SAS (version 9.4) using a PROC GLIMMIX for binary distribution with the mare's identity as a random effect.

The probability of pregnancy disruption was significantly higher when the mare was in one enclosure, while the male or males stayed in adjacent enclosure in comparison to when the mare was sharing enclosure with home stallion and/or geldings or when the mare was sharing enclosure only with mares. In agreement with our prediction, the proportion of pregnancies which were blocked or disrupted was lowest when away-mated mares returned home to an environment containing only other mares (**Figure 5**). Perhaps surprisingly, the frequency of pregnancy disruption in this category did not, however, differ significantly from the situation when away-mated mares were sharing enclosure with home males and could manipulate the male's paternity assessment.

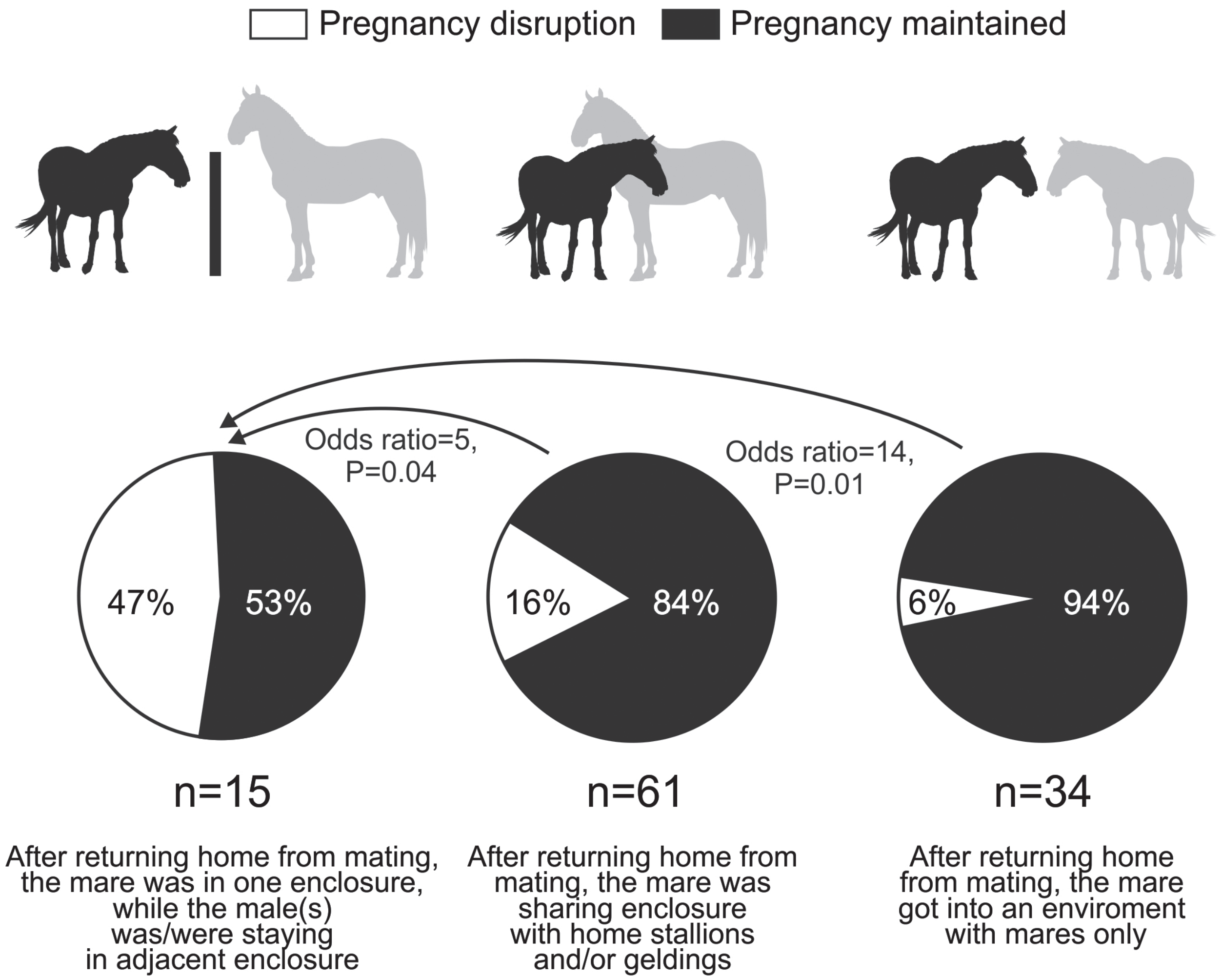

Figure 5. Proportion of pregnancy disruption according to social environment after returning to a home stable after mating and becoming pregnant elsewhere (reprinted from [60], permission for reuse provided by Elsevier).

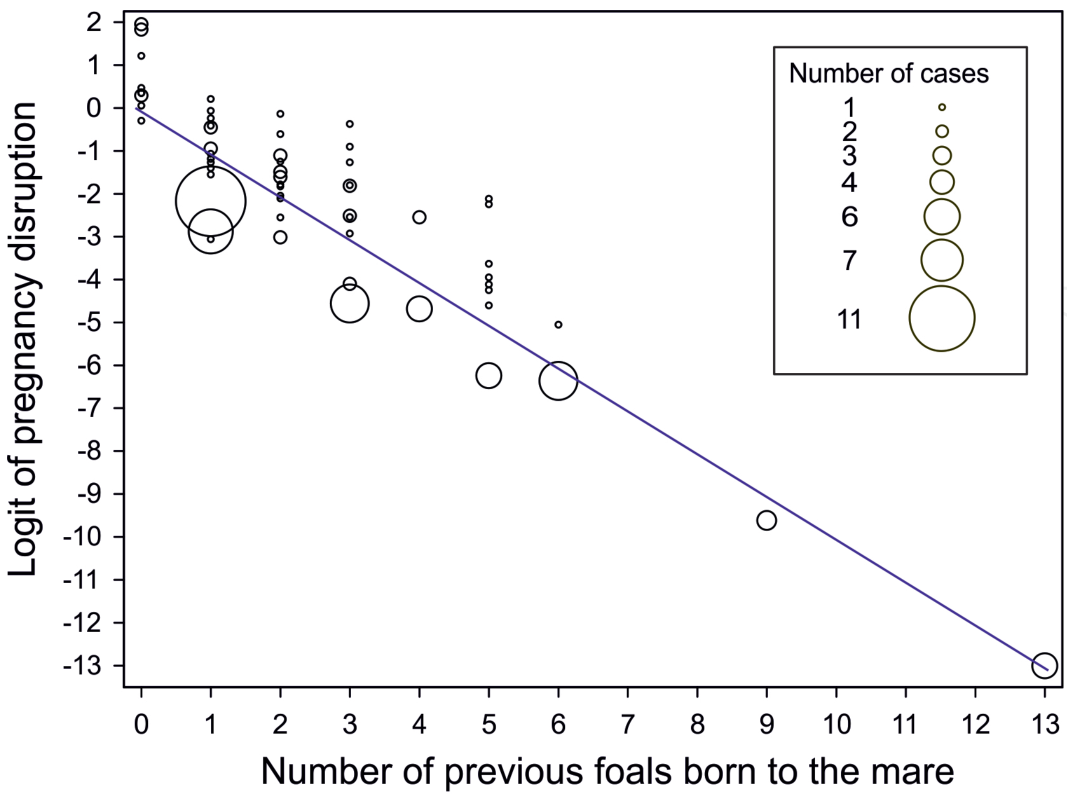

Figure 6. Probability of pregnancy disruption plotted against the number of previous foals born to the mare (reprinted from [60], permission for reuse provided by Elsevier).

When other factors were allowed to enter into the models only one other significant factor was found, the number of foals the mare had delivered in the past. With an increase in the number of foals delivered in her previous reproductive history the probability for the mare to disrupt pregnancy decreased (**Figure 6**).

4. Discussion

Taken together with the observation that the effect of social environment on pregnancy disruption was the same after artificial insemination, as with natural mattings away from home [59], strongly supports the original idea [48], that the primary factor modifying reproduction is a counterstrategy to the danger of potential infanticide [17]. In effect, whatever the method of insemination, once a mare is hormonally 'aware' of pregnancy, if she subsequently has no opportunity to mate with the home male (and thus confuse him about possible paternity), she will show increased likelihood of disrupting that pregnancy to avoid the costs of possible infanticide [compare also with 74]. An identical sociobiological origin of pregnancy failure has been recently shown in domestic dog *Canis lupus familiaris* [74]. In all three studies on domestic horse the probability of pregnancy disruption decreased with the number of foals a given mare had previously delivered (**Figures 2**, **4**, **6**). This fits well to the concept of

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residual reproductive value, which is equal to an organism's reproductive value in the next age interval [75]. Each offspring thus becomes more valuable to a mother as the number of future potential offspring declines over her lifetime [75–77]. Such a result strongly supports the original idea [48], that the primary factor modifying reproduction is a counterstrategy to the danger of potential infanticide [17].

As yet we do not know the mechanism by which pregnancy disruption may be induced. Nonetheless, it is possibly triggered by stress associated with the presence of a new male [review in [78]]. Stress has been suggested in many studies to cause aborts in animals and humans [e.g., [79, 80–82]].

Results of the described studies support generally the presumption that sociobiological effect leading to pregnancy block and/or disruption may explain substantial part of the high incidence of domestic horse fetal loss reported over decades [6–8, 83, 84].

During our 20 years lasting research of male infanticide in equids we found that the incidence of this phenomenon is affected by social organization and social environment of individual species. Domestic horse represents the species with high incidence of male infanticide in contrast to other domesticated ungulates. Nevertheless, this phenomenon involves a various counter-strategies which might affect the reproduction as we demonstrated here. Thus, the detailed knowledge of the sociobiology might lead to practical implications in holding and breeding of individual domesticated species; in our case domestic horse.

5. Conclusions

In conclusion, after either mating away of home environment [48] or AI [59], horse breeders should place the pregnant mare into the facility with no stallion(s)/gelding(s) [60] or to an enclosure together with the mare(s) to prevent pregnancy block and thus to improve production as well as welfare of horses [48, 59].

Non-genetic, especially environmental and social factors should be routinely involved in studies investigating causes of pregnancy loss besides reproductive health and veterinary aspects. Still it is not the case either in studies of reproductive success [85–87] or welfare of breeding horses [88] even after our first report was published [48].

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