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Harem stallion changes are not associated with diminished reproductive performance of females in semi-feral Konik polski horses (*Equus caballus*)

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ABSTRACT

Infanticide, related to a stallion's aggression toward a foal sired by another stallion, and feticide related to a new stallion's aggression and/or pheromonal influence (the Bruce effect) inducing loss of a fetus sired by another stallion, a female's counteraction to infanticide, have been proposed for domestic horses (*Equus caballus*) in human-managed conditions. The aim of the present study was, in conditions close to natural, to investigate the influence of the natural succession of a harem stallion on the mares' subsequent reproductive performance.

In a population of semi-feral Konik polski horses observed for 31 years (reproductive seasons) in 8 bands, harem stallion changed 10 times. These changes involved 26 out of 48 mares and 60 out of 609 observed mare-seasons (MS, a year in which a mare experienced a reproductive event). Binary distribution and log link function were assumed. The marginal model included the classification variable (SCH) and the continuous variables (age of the mare and calendar year of reproductive event (birth of a live foal, abortion, foals lost or barrenness) in a given MS was analyzed with generalized linear mixed model. The reproductive fitness of mares and their reproductive success (foal surviving $\geq$ 1 year), did not differ between MS with and without SCH. Older females were more likely to stay barren, with chances increasing by 21% with each successive year; and less likely to give birth to a foal (13% decrease of chance), and rear a foal to one year of age (12% decrease of chance). The age did not affect the probability of abortions.

Of the 26 MS when mares were pregnant when the stallion had changed, there were 25 healthy foals born. For the entire 31 years of monitoring, no aggression toward any foal was observed and all foals that were born in the harem of a new, succeeding stallion successfully reached adulthood.

Due to the lack of incidents of infanticide and the lack of evidence suggesting that the presence of a new harem stallion leads to the termination of pregnancies sired by another stallion, the Bruce effect was not confirmed as a biological strategy to reduce investment in pregnancy and potential infanticide in studied population of semi-feral horses.

1. Introduction

Equine reproductive biology and mechanisms underlying reproductive success are still far from being well understood. In conditions closed to natural, horses usually achieve high reproductive performance [1]. However, in human-controlled conditions, the mares may experience reduced pregnancy rate due to various factors [2,3], among which are sub-optimal conditions for expression of normal behavior [4,5]. Decreased libido in stallions [4], silent estrus, equivocal agonistic behavior during pregnancy or

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pseudo-receptive behavior in early pregnancy in mares [6,7] may mislead breeders, especially when ultrasound examination is not a routine stud practice. Also, other behavioral mechanisms such as infanticide and feticide are proposed to be responsible for decreased pregnancy rates in mares [8–10].

Infanticide and feticide, two phenomena related to a male's aggression potentially enhancing his reproductive success, have been suggested for several mammalian species [11–25], including wild equids [16,26]. Infanticide is defined as killing vulnerable infants by a male who has not sired them, especially after taking over a group of females [16,20,23]. The rationale for this male behavior is that it brings direct benefits, such as the more rapid return of the female to fertility than would not otherwise occur or the prevention of misled parental care [20].

In feral horses, only single cases of stallions killing foals have been described [13,16,18]. Moreover, the observed cases of stallions' infanticide occurred mainly under unstable conditions such as high population density [16] or in populations in which stallions were released only occasionally to breed with mares during the reproductive season [13].

Another potential aggression-related mechanism – termination of early pregnancy in females exposed to an unfamiliar male or its chemical signals ('Bruce effect') – is believed to be females' counterstrategy to male infanticide [19,20]. The Bruce effect was first observed and described in mice [27–29]. Since the costs of pregnancy and offspring upbringing are high for females, terminating a pregnancy sired by a predecessor prevents energy waste in production of offspring that most likely will be lost due to possible infanticide of successor males. The Bruce effect has been studied and described thoroughly in rodents; however, observations have also been performed for other species [9,14,30–33]. In a feral horse population, Berger [34] observed forced copulations by stallions when taking over a band of mares that he concluded led to abortions of early pregnancies. However, such behavior has not been described by any other author. Recently, questionnaire-based surveys of horse owners were conducted for domestic mares [8–10]. The results suggest that mares inseminated away from home, either naturally or artificially, were at higher risk of abortion after returning home compared to mares pregnant from the home stallion, especially when they experienced contact with a male separated by a fence. In this case, as suggested by latter authors, the mare cannot confuse the home stallion about his paternity, which may occur when she is placed in the same enclosure as the home stallion, so she " 'manipulates' the male's paternity assessment by promiscuous mating (which) may explain a common increased incidence of foetal loss in domestic horses" [8]. In contrast, Asa et al. [35], who observed a group of pregnant mares with a stallion that had not sired their pregnancies, never noticed such cases. Clearly, except for the cited studies, there is still much to learn about the drivers of variation in female reproduction in free-roaming horses.

The aim of the present study was, in conditions close to natural, to investigate the negative influence of the succession of a new harem stallion on the mares' subsequent reproductive performance. We discussed the concept of potential infanticide and feticide in horses [8–10,13,16,18] regarding the hypothetical reproductive benefits. We hypothesize that if both infanticide and feticide occur in horses, the reproductive fitness of mares measured in terms of the numbers of abortions, foals born, and foals that survived $\geq$ one year will differ before and after stallion takeovers of the mares or after mare's migration. With direct observation, we can document stallions' aggression toward foals and forced or allowed copulations with pregnant mares. To investigate our hypotheses, we reviewed the database from 31 years detailing the migration and reproduction of a herd of Konik polski horses managed under semi-feral conditions. Such a long timeframe of observations provides detailed information about reproductive events. Considering the longevity of horses up to 30 years or greater, these records spanned the lifetimes of many of individuals.

2. Material and methods

2.1. Ethical note

The study involved the analysis of breeding records and regular observations of animals from a distance. No experimentation was performed given European directive 2010/63/EU and the Polish laws related to ethics in animal experimentation. The animals were under the care of the staff of the Experimental Station of Polish Academy of Science in Popielno, Poland.

2.2. Study site

Between 1986 and 2017 semi-feral Konik polski horses were observed daily in their sanctuary situated on a peninsula in northeastern Poland by one of the coauthors (ZJ). Konik polski horses were introduced to the sanctuary in 1956 as probable descendants of extinct Tarpans (*Equus caballus gmellini Ant. forma silvatica Vet.*) to experimentally prove their adaptability to and survival in natural East European environmental conditions [1,36,37]. The available area is 16.2 km^2 of forests, some grassland, and wetlands. The sanctuary is surrounded on the east and west by lakes, which are natural borders. On the north and the south, the sanctuary is fenced. With annual surplus offspring removal, the habitat meets the nutritional and spatial needs of all horses throughout the year, limiting the influences of ecological pressures such as feed shortage or a high stocking rate on social structure of herds.

2.3. Animals

For the present study we defined a "harem" as a social group of an individual stallion and his mares (male-females group) while as a "band" we define a stable group of mares that can be harems of several stallions in case they change. Horses run freely and are unmanaged except for the annual removal of young offspring due to restricted area available to horses. Some colts and fillies are left for parents' replacement. When remaining in the herd, young horses naturally disperse from the natal group, usually at the age of 25 months ± 11 months. Male offspring generally remain in their natal harem band longer than young females. Sporadically, new horses from other sanctuaries are introduced. For approximately ten generations, this system has ensured the persistence of the population with minimal inbreeding. Individual horses are recognized based on markings and freeze brands. The horses live in distinct, freely formed bands. The succession of harem males occurs as a result of fights between stallions, mostly between a young stallion and its sire. In the majority of cases, the defeated stallion dies in the following months. Young mares are accepted by another stallion, and their lifetimes often reach 25 years or more (up to 34 years old for the most long-lived mare).

Over the 31 years of this study, the number of separate harem bands in the sanctuary at any one time ranged from three to five. Each band consisted of 1–10 mares and one stallion. No multi-stallion or bachelor groups were formed during the observation period. Altogether 8 bands, 11 harems, 11 stallions and 50 mares were observed and recorded. All horses are under a genetic resources protection program according to the Convention on Biological Diversity (https://www.cbd.int/) and are entered in the Konik polski studbook.

All dates of birth and death of the horses in the sanctuary were

recorded. Additionally, the dates of the introduction of new horses were noted. The parents were recorded for each newborn foal; additionally, the parentage was genetically confirmed in a laboratory certified by ISAG (International Society of Animal Genetics). There was no discrepancy in parentage assignment between the manager and genetic assessment. The records also included, for each group, all cases of harem stallion change resulting from a harem stallion death or fight, the assignment of mares to a given stallion and the migration of mares from the natal band (forced) and between bands as adults (voluntary). During monitoring, observed estrous signs, matings, changes in harem and band composition, and all cases of birth, and death were noted.

2.4. Breeding records

Stallion change (SCH) is defined as a situation in which the stallion was succeeded by another one within the same group of mares or a mare had migrated (changed the harem voluntarily or as result of natal dispersal).

For each mare, the mare-seasons (MS), i.e. reproductive units (calendar years) in which a mare experienced a reproductive event (foaling, abortion, foal loss), was reviewed for the whole life or until 2017 (for dead and alive individuals, respectively). The death cause of individual foals was inspected for cases of infanticide (general necropsy for evidence of external and internal signs of physical abuse). Since the stallions changed usually for a group of mares, one SCH is reflected in a given MS of several mares.

To assess the effect of stallion change, mares' reproductive fitness per MS included the following outcomes (yes/no):

- foal born live;
- barrenness (defined as no pregnancy in a given reproductive season)
- abortion (defined as pregnancy loss after the 40th day of pregnancy, only in cases in which we could see or find the fetus);
- reproductive success (foal raised to 1 year of age);

To assign reproductive indices to the above classification, we used the method based on conception-to-foaling duration (in days). To calculate the probable conception date, we assumed that first postpartum estrus (foal heat) occurred within 8–14 days and that pregnancy lasted 325 days [38]. First mating season of the maiden fillies was treated as MS0 and was not taken for calculations as its result could be observed the next year (season). Also, two mares with evident clinical signs of reproductive dysfunctions (throughout the observation period they got pregnant and gave birth only to two per 12 MS and six per 27 MS foals respectively) were excluded from the studied population since we focused on behavioral infertility only.

2.5. Statistical analyses

The effect of SCH on the probability of the occurrence of the reproductive event of mares (foals born alive, reproductive success, abortion, and barrenness per MS) was evaluated with the generalized linear mixed model (PROC GLIMMIX, SAS 9.4 Statistical Package). As the dependent variables have a binary outcome, a binary distribution and log link function were assumed. The marginal model included the classification variable (SCH) and the continuous variables (age of the mare and calendar year of reproductive event). Logit scale parameter estimates (coefficient, Co) and odds ratio (OR) were presented for foals born alive, reproductive success, abortion, and barrenness. Effect of age was reported as the mean probability (LSM ± SE) of foals born alive, reproductive success, abortion, and barrenness. Effect of the increasing age of the mare (by one year) to deliver live foals, reproductive success, abortion and barrenness was given in percent. The mare nested in band was considered a residual random effect with a compound symmetry covariance structure. A pseudo-likelihood estimation method and the empirical Sandwich estimates for the standard error of the fixed effects were used. Average number of foals born per mare was presented as mean ± SD.

Data used for the calculations are presented in the Supplementary Material 1.

3. Results

3.1. Stallion changes

A total of 609 mare-seasons (MS) for 48 mares were recorded. In total, SCH in 10 harems were recorded. On average, a mare changed harem stallion 0.8 ± 1.0 times (range: 0–3 times), and regarding whether the mare was dead or alive at the moment of database formation (2017) 0.7 ± 1.0 and 1.0 ± 1.0 times, respectively. Twenty-three mares experienced no SCH, 25 experienced at least one SCH: 15 mares one SCH, 5 mares two SCH and 5 mares three SCH.

3.2. Reproductive performance of mares

Altogether, 443 foals were born during the 31 years. No effect of calendar year upon reproductive efficiency: foal born alive (Co = 0.01, F = 0.33, P > 0.05), barrenness (Co = -0.02, F = 1.31, P > 0.05), abortions (Co = -0.01, F = 0.12, P > 0.05) and reproductive success (Co = 0.02, F = 0.40, P > 0.05) was stated. The majority (419) of foals survived either until their removal from the sanctuary (when the foals were approximately 7–9 months old) or at least until one year old in cases they remained in the sanctuary. Twenty-four foals died before 1 year of age due to congenital defects and/or disease (14 foals), natal isoerythrolysis (five foals), in accidents (two foals), and three were stillborn. The average number of foals born and raised per mare amounted to 9.0 ± 6.7 and 8.6 ± 6.3, respectively. Notably, within the observed timeframe and according to the age at database formation, some mares did not raise any or raised just one foal (eight very young or very old mares) and some raised 18 foals (five mares), with the most outstanding mare raising 24 foals.

3.3. Stallion change and the reproductive performance of mares

During the breeding seasons in which the stallion changed, there were 26 MS when mares were pregnant and nine MS when mares were barren; in the cases of the other seven MS, we were not able to diagnose the pregnancy in investigated mares with 100% certainty. Out of these 26 pregnancies, there were 24 healthy foals born, one mare gave birth to a healthy foal that was killed in a car accident in its 1st week of life, and one mare aborted. This particular mare was 22 years old and had previous reproductive problems: she aborted the year before, and the aforementioned abortion (in approximately the 7th month of pregnancy) occurred three months after the band had been taken over by a new stallion.

The reproductive fitness of a mare in the season following SCH, as compared to socially stable seasons, did not differ for the probability of giving birth to live foal (SCH seasons: 0.86 ± 0.07 vs. stable seasons: 0.91 ± 0.02, F = 0.81, P > 0.05; OR = 1.63), to abort (0.04 ± 0.03 vs. 0.03 ± 0.01, F = 0.45, P > 0.05; OR = 0.58), to stay barren (0.10 ± 0.05 vs. 0.06 ± 0.02, F = 2.15, P > 0.05; OR = 0.52) or to have a reproductive success in a given season (0.79 ± 0.07 vs. 0.85 ± 0.02, F = 0.79, P > 0.05; OR = 1.45).

Among 443 healthy foals, 28 were born in the harem of a new, succeeding stallion. All of these foals successfully reached

adulthood. No forced copulations or copulations allowed by pregnant mares were ever witnessed. Additionally, no cases of stallion aggression toward pregnant mares or foals sired by other stallions were observed.

3.4. Age effect

Older females were more likely to stay barren (Co = 0.19, F = 20.5, P < 0.0001), with chances increasing by 21% with each successive year; and less likely to give birth to a foal (Co = -0.13, F = 12.0, P < 0.0001, 13% decrease of chance), and rear a foal to one year of age (Co = -0.13, F = 24.7, P < 0.0001, 12% decrease of chance). The age did not affect the probability of abortions (Co = 0.04, F = 1.31, P > 0.05).

Detailed reports for the seven mares for which we were not able to classify the reproductive status at the moment of SCH is presented in Supplementary Table 1. Of these mares, five gave birth to a foal sired by a new stallion in the year following the stallion change.

4. Discussion

Our analyses showed that the seasonal reproductive fitness of observed mares was similar whether a mare experienced harem stallion change or not. An important factor challenging mare's reproduction was an advanced age. Since age is widely recognized as adversely affecting reproduction and has been extensively studied [39–44], in the present work we focus on mechanisms of purported male-provoked subfertility in mares. The analysis of reproductive records of Koniks population does not support the hypothesis of the Bruce effect in semi-feral horses with two findings: infanticide as underlying cause of early pregnancy failure was never observed, and the negative effect of a stallion change on reproductive performance of mares was not detected.

4.1. Male infanticide

It was proposed that the potential gains from infanticide are: using the neonate as a resource (i.e. as food), elimination of the potential competitor for resources, enhanced reproductive success of a partner and the "increased access for individuals of one sex for reproductive investment by the other sex at the expense of same-sex competitors" [12]. However, any of the suggested reasons, including the last one assumed as rationale for decreased reproductive performance in domestic mare [8–10], was not observed in studied population.

Infanticide is believed to bring direct benefits to the male due to the faster return of the female to fertility [20,23]. In the case of horses, mares start cycling within 8–14 days *postpartum* and remain fertile the entire breeding season [45]. Thus, killing the newborn foal would not change the mare's fertility and might be pointless in terms of male's reproductive benefit. In contrast to lions and other animal species, for which infanticide may serve some biological functions and has been observed in nature [46–50], no rationale for such a mechanism is evident neither in domestic horses under natural conditions nor in Przewalski horses after infanticide [16].

Observations of Feh and Munkhtuya [16] showed that Przewalski mares whose foals were sporadically killed did not allow breeding with the infanticidal stallions. Therefore, these stallions did not gain any reproductive benefits from the infanticide, as has been postulated for other species. Since in wild equids males' incidental infanticide is observed towards unrelated but also related foals [16] a pathological social behavior rather than a reproductive strategy in horses was proposed as explanation [16]. Moreover, it can be hypothesized that wild equids, especially zebra, have a generally higher level of aggression, especially toward neonates [51] of own and other species like antelopes [52]. Importantly, no infanticide was confirmed by our study, as none of 443 foals was killed by a stallion over 30 years of observations; although the harassment of adults by other stallions present in the sanctuary and the succession of stallions occurred spontaneously, and the animals were free to choose sexual partners from available groups within the sanctuary. No attacks of a new stallion on newborn foals sired by the previous stallion or on any other foals were ever witnessed or confirmed with the necropsy of dead foals. In the observed population, twenty-eight foals were born after takeovers, and all of them successfully reached adulthood. Additionally, we observed that when these foals were left in the sanctuary, the stallion expelled unrelated immature horses as in case of own offspring as reported by other studies [53]. Twenty-five years of daily observations of the University of Pennsylvania's semi-feral pony herd have shown that of 375 foals born into that herd, 66 neonates have been with harem stallions that were not their sire (McDonnell, personal communication). No infanticide or aggressive behavior of stallions to foals has been observed and detailed focal observations have similarly indicated no difference in parenting behavior of harem stallions toward sired and non-sired foals in their band (McDonnell, personal communication). In the studied population, the finding that no foals were lost due to male aggression compared to 24 foals lost for other reasons before 1 year of age, questions the hypothesis that mares have to employ any strategy to avoid foal loss due to possible infanticide [8–10]. Hitherto results on possible Bruce effect in domestic mares were based on questionnaires filled by owners of mares kept in stabling conditions [8–10,13,16,18] with no direct observation of the animals' behavior. Comparing to our results including regular inspection and behavior observations, we think that the question of whether females' reproductive counterstrategy to infanticide, i.e., the Bruce effect, has any biological rationale in domestic mares remains open and requires further research.

4.2. Bruce effect

Previous studies [8–10] imply that mares, similar to mice, may terminate pregnancy in the presence of a male that did not sire the fetus, especially when a female has not the direct access to the dominant male. The pregnancy rate was compared between mares mated or inseminated with home or unfamiliar stallions. The results suggest that when a mare was bred with an unfamiliar stallion and then kept in an enclosure adjacent to a home stallion or gelding, the probability of pregnancy termination was the highest. However, the distribution of factors between compared groups that undoubtedly influence the reproductive performance, such as age, detailed reproductive and veterinary history of mares, use of pregnancy diagnostic technique (palpation or ultrasound examination since the questionnaire reaches back to the 1980s, when the use of ultrasound was uncommon), possible differences in feeding, stage of pregnancy after returning home [8–10], in which the placentation is one of the critical points [54], or the method of insemination (natural or artificial, the latter often including hormonal treatment) [8,10], were not given. In general, the pregnancy rate in domestically managed mares is approximately 60–69% per cycle [41,55]. Factors influencing conception and embryo development, including the signal of maternal recognition of pregnancy, are still not elucidated in horses [41,53,56]. Thus, without a scrutinized follow-up of the mare's reproductive history, behavior observations, and physiological and health status examinations, it may be difficult to interpret the results. A detailed analysis of the collected data yielded a large amount of relevant information in our

study (Supplementary Table 1). The problematic cases (barrenness) following stallion change involved mare's congenital subfertility, advanced age, refusal to be mated by a son, poor post-winter condition and the refusal to be mated by a new stallion. Such information sheds additional light on the interpretation of potential causes of barrenness.

4.3. Misleading parental care

It has been proposed that mares manipulate their pregnancy status to avoid potential infanticide when not able to mislead a dominant male about his paternity [8]. In our study, three mares with evident reproductive problems, including serological incompatibility with the stallion, did not leave the harem to join a new stallion with whom they could improve the reproductive outcome. Based on this observation we speculate that mares may not be able to predict the outcomes of their pregnancies to counteract possible loss, and manipulate the pregnancy outcome.

We acknowledge that the only human intervention, the annual removal of almost all born offspring, may have disturbed the natural composition of groups present in the sanctuary. Thus, the distribution of males and females of different ages is not completely natural and may affect the outcomes of the present study. However, to our knowledge, there is actually no completely natural (feralised) domestic horse population that would not be managed somehow (by area restriction, surplus young removal or contraception) otherwise it leads either to overpopulation or unnatural reduction of fertility. The example of the catastrophic outcome of uncontrolled reproduction of horses in a reserve where unlimited reproduction on limited area resulted in deaths of over half of the animals, mostly from starvation [57] shows that with no predators' harassment, present populations of feral horses have to be managed somehow in order to maintain the horses' welfare. It is proposed that feed availability is a probable reason for the formation of separate harems [58]. Also, in polygynous ungulates, the sex ratio is expected to be biased toward females [53] due to higher dispersal mortality of expelled males travelling to novel places in unrestricted areas. Nevertheless, the sanctuary area is limited, and the welfare of the horses is a priority, as a high stocking rate of horses would influence their behavior and condition. In such a case, the collected data might not reflect the natural behavior of horses but rather pathological one caused by shortages of food and space [4,16,59–61].

We recognize that another issue which could potentially bias the results is the frequency of stallion changes. Available literatures as well as our own observations indicate that a harem stallion manages a group of mares as long as he is able to defend them from other stallions [62,63]. This period may significantly differ from stallion to stallion because the factors such as feed and water availability, presence of other stallions, stallion's age, its qualities or random accidents may influence the leadership [52,62,63]. To our knowledge there is no reference research on average/routine feral stallion change and we believe that observational period of more than 30 years evidences for the first time how frequent changes of harem stallions are. Every SCH in our study occurred by defeating the predecessor harem stallion by the successor, that is as it has been reported for other feral populations. Hence, we think that the number of SCH in our study may reflect natural situation in feral equine population.

5. Conclusions

Due to the lack of incidents of infanticide and the lack of evidence that the presence of a new stallion leads to the termination of pregnancies sires by another stallion, our results suggest that the Bruce effect is unlikely to be a biological strategy to reduce investment in pregnancy and prevent potential infanticide in horses. No benefits underlying such mechanism were evidenced in horses living in semi-feral groups. Thus, our findings do not support the concepts of both infanticide and feticide (the Bruce effect) in *Equus caballus*, as they did not occur and seemed to have no biological justification, as shown by our long-term studies involving semi-feral horses. However, the limited number of closely monitored animals in feral groups, as well as subject-related research and contradictory results encourage further investigation of these phenomena in *Equus caballus* species.

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Declaration of competing interest

We declare that there is no conflict of interest that could be perceived as prejudicing the impartiality of the research reported.

CRediT authorship contribution statement

Joanna Jaworska: Conceptualization, Methodology, Investigation, Resources, Writing - original draft, Writing - review & editing, Formal analysis, Funding acquisition, Project administration. **Zbigniew Jaworski:** Conceptualization, Resources, Investigation, Validation. **Sue M. McDonnell:** Conceptualization, Writing - review & editing, Validation. **Aleksandra Górecka-Bruzda:** Conceptualization, Methodology, Software, Writing - original draft, Writing - review & editing, Formal analysis, Supervision.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.theriogenology.2020.03.033.

Authors' contributions

JJ analyzed the data and wrote the manuscript. ZJ collected and analyzed the data. SMM contributed to the data analysis and manuscript preparation. AGB supervised the work and contributed to the data analysis and manuscript writing and preparation. All authors critically revised and approved the final version of the manuscript.

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