The social organisation of natural herds of koniks (*Equus caballus*): subordinate stallions, rule or exception?

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Abstract: This article describes the social organisation of herds of free-roaming koniks in the Netherlands and elsewhere in Europe, with a particular focus on the Oostvaardersplassen. Attention is directed to: 1. Herd size in relation to habitat conditions. 2. Composition of harems within those herds. 3. The role and relative number of subordinate stallions in those harems. On the basis of this information, the article subsequently describes the assumed situation regarding subordinate stallions at the Oostvaardersplassen and in other areas with large herds of free-roaming horses. Following this, the validity of this assumption is investigated for other konik grazing areas within the Netherlands, using field data that also include those from a repeated study about the Oostvaardersplassen. Finally, it is investigated whether the outcome also applies to feral horses (*Equus caballus*), Przewalski's horses (*Equus przewalskii*), zebras and African and Asiatic wild asses (*Equus spp.*) elsewhere in the world. The free-roaming koniks in Europe, in contrast to those elsewhere in the world, mostly live in nature areas that are rich in food and have an ample drinking water supply. In such areas, koniks appear to prefer to live in large groups. The ample food supply in the areas studied supports such large herds. In two other areas that were less rich in food, the harems opted to live separately. Large herds were also often found to break up into smaller herds in the wintertime, when food would become scarce. Exclusive home ranges with only one harem were found in certain areas with narrow road crossings or traversable dykes, or in long and narrow areas. Exclusive home ranges are different from true territories, as only the harems were defended, rather than the land itself. Thus, independent harems or groups can be formed not only as a result of food scarcity but also because of the type of terrain. Free-roaming koniks, in Europe, live in herds with a social organisation of harems and bachelor groups that is similar to elsewhere in the world among wild Equidae and feral horses. In Europe, however, this organisation can only be observed in nature areas with larger herds that live in an autonomously chosen social structure - thus, in areas with only limited human intervention. The presence of multiple harems, however, does mean that dominant stallions continually need to fend off the competition. This is why harems in such large herds often have a particular composition in which subordinate stallions also play an important role, in addition to the dominant stallion, both in tasks and numbers. Having subordinate stallions around offers advantages; they help to defend the harem and, thus, contribute to achieving the much-needed peace and quiet for mares and their foals. Subordinate stallions also help to prevent predation, and larger numbers of subordinate stallions are seen in situations of increased risk of predation. Subordinate stallions themselves, however, experience only few advantages in relation to their efforts. Thus, among the free-roaming koniks studied, there appeared to be no mutualism or altruism. Subordinate stallions and dominant stallions do appear to have different temperaments. Predation also seems to lead to the formation of large groups as well as to increased collaboration between stallions, although this is not - yet - the case in the Dutch situation. The occurrence of subordinate stallions, therefore, is the rule rather than the exception, and appears to be

related to herd size, the presence of rivalling stallions, predation and food supply.

Keywords: feral horse, social and spatial organisation, herd formation, dominant stallion, subordinate stallion, multi-stallion harem, Oostvaardersplassen, konik, free-roaming horse.

Introduction

There are bovines and horses in numerous nature areas in the Netherlands. In some cases, these are animals of the same gender and age that have been brought into the area for one season, but often they are free-roaming* animals living in natural herds, or a composition in between. Particularly the herds of free-roaming animals are provided with enough space to demonstrate their natural behaviour, such as in the case of the bovines and horses at the Oostvaardersplassen and various nature areas where large grazers are being managed by the FREE Nature organisation (the Dutch Foundation for Restoring European Ecosystems). Animals in those areas are often found to organise themselves into social herd structures. However, the degree to which this is natural behaviour and whether the behaviour is similar to that of the horse's original wild ancestor (*Equus caballus*) is unknown. The enormous herd of koniks at the Oostvaardersplassen, in particular, with its complex social organisation, is often viewed as the exception to the rule. Since 2008, this area has been home to a single large herd that, at the start of each summer season, contains around 900 animals over the age of one, as well as around 250 foals (Cornelissen et al. 2016). We set out to determine whether the Oostvaardersplassen are indeed an exception in this respect. This article describes both literature and field research into the social organisation of herds of free-roaming koniks, in the Netherlands and elsewhere in Europe, with a particular focus on the Oostvaardersplassen.

To obtain a greater insight into the importance of herds for Equidae in general, we focused our attention on: 1. Herd size in relation to habitat conditions. 2. The social organisation of herds, particularly the composition of the harems that are part of those herds. 3. The relative number of subordinate stallions and their role within those harems. On the basis of this information, we were then able to create an image of the assumed situation of subordinate stallions at the Oostvaardersplassen, as well as in other areas with large herds of free-roaming horses. Subsequently, we investigated whether this image also applied to other areas with herds of koniks in the Netherlands. To this end, we used field data that also included results from repeated research in the Oostvaardersplassen. Finally, we examined whether our results also apply to feral horses (*Equus caballus),* Przewalski's horses (*Equus przewalskii*), zebras and African and Asiatic wild asses (*Equus* spp.), elsewhere in the world.

* The koniks living in herds in nature areas in the Netherlands are sometimes characterised as *wild* horses. However, as long as herds are under human management, it would be more accurate to speak of *free-roaming* horses. Since these horses still have a known owner, they cannot be called *feral* horses like the mustangs and brumbies in North-America and Australia. In fact, in the Netherlands, only the Oostvaardersplassen contain herds of what could be considered *wild* horses, as human intervention there is limited to the culling of animals that would not have survived anyway.

Habitat conditions

Large herds have been observed to occur among all species of Equidae, ranging from hundreds of animals to over a thousand per herd (Berger 1986, Rubenstein 2011). Large herds often exist only temporarily, and mostly stay in locations with ample supplies of water

and high quality food (Rubenstein 2011). For those species that form harems, such as plains zebras (*Equus quagga*) and Mongolian wild asses (*Equus hemionus hemionus*), such herds were found to always consist of a conglomerate of harems and bachelor groups (Feh et al. 2001, Rubenstein 2011). Living in groups provides protection against predators (Rubenstein 2011), and this behaviour can still be seen in feral horses today — even though they have not been confronted with predators for generations (Rubenstein 2014). Living in groups not only reduces the individual risk of predation, it also means that a larger number of animals are available to keep watch, which increases the predator discovery rate, and, on balance, provides individual animals with more grazing time. In addition, herd formation offers protection in times of bad weather, and may help drive off bands of bachelor stallions (Rubenstein 2011). Bachelor or solitary stallions are adult males without a harem, who attempt to increase their chances of procreation by servicing or taking over mares from existing harems.

The degree of herd formation among plains zebras in Africa depends on the size of the bachelor bands trying to take over or service the mares. In such cases, stallions from various harems have been observed to collaborate, in order to chase larger groups of bachelor stallions away (Rubenstein 2011, Rubenstein 2014). Studies on plains zebras and Mongolian wild asses (Bahloul 2001, Feh et al. 2001, Rubenstein 2011) have shown food availability not to affect herd formation, although having an ample food supply nearby is one of the characteristics of the locations in which herds are staying. Most wild Equidae and feral horses outside Europe live in oligotrophic ecosystems with a short growth season (Berger 1986), and in lower densities than those in more nutrient-rich European nature areas that, in addition, have a mild climate and usually an ample drinking water supply. In the Netherlands, most konik herds also roam nutrient-rich soils, such as floodplains and reclaimed marine clay areas that have a relatively long growth season (nine months), as well. The ample food supply and resulting lack of food competition means these areas are able to sustain large herd sizes, without herds needing to break up. However, as yet unclear is the precise mechanism that causes these Equidae to live in large groups.

Social organisation: herds and harems

Wild Equidae live in herds of various social structures, which largely depend on the characteristics of their habitat (see previous section). For example, in predator-poor, semi-desert areas, the stallions of feral donkeys (*Equus africanus)* and onagers (*Equus hemionus*) in low-predation, semi-dessert areas in Israel and India, and Grévy's zebras (*Equus grevyi*) in Africa, have territories that they defend against congeners, and bands of mares travel along these territories looking for food and water (Feh et al. 2001, Rubenstein 2011, 2014, Ransom & Kaczensky 2016). The strongest stallions have the best territories and therefore are most frequently visited by mares.

In regions with moderate precipitation levels, the Equidae generally live in harems, such as the plains zebras in Africa (Rubenstein 2011), the Camargue horses in France (Duncan 1992), the feral horses in North America, New Zealand and Australia (Ransom & Kaczensky 2016), and the Przewalski's horses in Mongolia (Wit et al. 2006). Such harems typically consist of a dominant stallion and multiple mares with young offspring. Dominant stallions can be described as stallions in charge of their harem, who have the first choice of which mares to service. This is why, often, most of the foals in a harem are sired by the dominant stallion. The members of a harem stick together, and dominant stallions defend their harem against rivals. Mares prefer a steady harem with a dominant stallion, to ensure they can graze in peace and stay in a good physical condition (Rubenstein 2011,

2014). Young animals usually leave the harem when they become sexually mature, forming bachelor groups or temporary groups of adolescents (Berger 1986, 1987, Rubenstein 2011, Ransom & Kaczensky 2016). Harem home ranges usually overlap; however, in certain circumstances, harems can be territorial, such as is described about Shackleford Island (Rubenstein 1981, 2014). On this island, food and water are widely spread and the sea forms a natural boundary, which means stallions only need to defend the land side of their territory. The island has also been observed to contain groups of varying compositions (Rubenstein 1981), which is rare in feral horses elsewhere.

Mongolian wild asses in Turkmenistan and Mongolia show both types of behaviour (Feh et al. 2001). In areas of predation by wolves, harems are the norm, and groups consisting of only female animals and their young are rare, whereas the latter is found more often in regions where wolves are hardly seen (Feh et al. 2001). Mongolian wild asses, therefore, also appear to adjust their social organisation to habitat conditions.

Subordinate stallions

A phenomenon related to the social organisation of Equidae herds that has not yet been described for Europe is that of subordinate stallions. These adult stallions are harem members, who are subordinate to the dominant stallion. The main role of these subordinate stallions is that of defending the harem against other stallions. Subordinate stallions are often found in harems of feral horses in North America, New Zealand and Australia (Berger 1986, Linklater 1998, Ransom & Kaczensky 2016).

Although the dominant stallion usually sires the foals, subordinate stallions were also found to have sired foals, on occasion. These subordinate stallions not only do the hard work, they are able to reproduce as well, and, thus, also benefit from their position within the herd. However, these benefits seem relatively limited. In herds of feral horses in New Zealand, subordinate stallions and bachelor stallions were found to have about equal access to mares in the harems (Linklater 1998). Populations of feral horses were also found to include harems with two dominant stallions, in addition to those with subordinate stallions. In such cases, the dominant stallions were seen to work together to defend their harem (Rubenstein 2011, Ransom & Kaczensky 2016). Often, such collaborations are already formed when they are still within the bachelor groups. Their relationship is one of equals, with both stallions participating in procreation and neither being subordinate to the other.

The literature does describe collaborations between dominant stallions from different harems in herds of wild Equidae, but there is no mention of harems with subordinate stallions. For example, no subordinate stallions have been observed in herds of wild Przewalski's horses in the Hustain Nuruu National Park in Mongolia (Feh et al. 2001). Feh et al. (2001) do describe harems of Mongolian wild asses with more than one stallion, but not whether there are any subordinate stallions. It can be deduced from their article that these stallions concern both youngsters and more mature stallions. Bahloul (2001) also mentions the occurrence of steady groups of Mongolian wild asses with one or two stallions, which may point to the presence of subordinate stallions.

Oostvaardersplassen

The herd of koniks at the Oostvaardersplassen is the only truly wild herd of horses in Europe of which the social organisation is not subject to human interference. The Oostvaardersplassen population basically consists of one large herd roaming the area. This large herd is subdivided into numerous harems containing many subordinate stallions. Bachelor groups, older solitary bachelor stallions and temporary associations of young males and females are an integral part of this herd (Nieuwdorp 1998).

It is expected that the structure of this herd is not unique, but that the nutrient-rich environment in the Netherlands would in fact be able to support other large herds of horses with harems that contain substantial numbers of subordinate stallions. It is assumed that the presence of multiple harems within one herd means that dominant stallions continually need to fend off the competition. Subordinate stallions are a godsend, in those circumstances; they help to defend the harem and thus contribute to achieving the needed rest for mares and their foals.

This article investigates whether both these assumptions are correct, and, if so, whether they provide more insight into the social organisation of free-roaming herds of koniks in the Netherlands.

Method

Over the past 25 years, nature conservation organisations FREE Nature and ARK Nature have acquired a large amount of knowledge about free-roaming herds of koniks and how these are managed in various nature areas, both in the Netherlands and abroad. Since 1991, the ancestry of each individual animal is recorded in the herd database of FREE Nature, as well as the current and past roaming areas, the harem or bachelor group the animals belong to, and their position within the herd (dominant or subordinate stallion) and any changes in that position. In addition to field observations, ancestry research into the DNA of many animals has identified the dam as well as the sire of the animals, and in rare cases even revealed a foster mother. As DNA research has not been done for all animals, a foal's sire is sometimes unknown.

We used data from this database for the year 2013 for a more in-depth analysis, because of the relatively large size of the konik herds in that year, which resulted in a rather large amount of data available for analysis and interpretation. In 2013, around 400 koniks of FREE Nature were roaming 15 nature areas. From the information in the database, we determined the number of subordinate stallions per harem, as well as the ancestry of the foals that were born in the following year. In addition, the data helped to determine gender ratios within FREE Nature herds, as well as the herds' annual reproduction level. We approached the herd managers of FREE Nature and enquired about the occurrence of multiple, equally dominant stallions within a harem, and whether harems and bachelor groups would roam together or had separate territories and displayed territorial behaviour.

In order to compare the information with that on the Oostvaardersplassen, we looked at whether areas with large herds of koniks from FREE Nature had a different social organisation than areas with smaller herds. The larger the herd in a particular territory, the larger the number of outside competitors for harem stallions to fend off. If this fact would affect the number of subordinate stallions, then smaller herds were expected to have fewer subordinate stallions than larger herds. The line between small and large herds was drawn, more or less arbitrarily, at 25 koniks. Of the small herds, in 2013, there were eleven areas containing one harem each; larger herds were found in seven areas, mostly containing multiple harems per area (26 harems in total). We calculated the average number of subordinate stallions per harem, for both types of areas.

The co-author conducted a study, between February and June 1998, into the social organisation of herds of koniks at the Oostvaardersplassen (Nieuwdorp 1998). In the autumn of 2014, we returned to the Oostvaardersplassen to investigate whether the social organisation of 1998 was still in place, 16 years later. To this end, during one day in 2014, we counted the adult stallions in the harems of a part of the herd. On that day, we counted over 500 horses of the total herd of around 1150; a 40% sample of the total number of koniks at the Oostvaardersplassen at the time. The other koniks could not be counted because they

Fighting konik stallions. Oostvaardersplassen, 29 November 2014. *Photo: Leo Linnartz.*

were in one large group, in a location that was difficult to access. Of the 58 harems in the counted part of the herd, we documented the size of the harems and the number of adult stallions within them. In addition, we observed where the harems were located in relation to the rest of the counted herd. We also saw stallions that did not belong to any harems, but we did not count those.

Rubenstein (2011) also - and elaborately - includes ethological aspects in describing the systematics of Equidae species and subspecies. As these aspects were also explicitly included in our study, we follow Rubenstein's opinions about systematics and scientific nomenclature.

Results

The herds of FREE Nature

Predominantly in a single herd

The FREE Nature herds of free-roaming koniks, generally, consist of single, large groups per area, all year round. In 2013, this was the situation in 12 of the 15 FREE Nature areas. In Groenlanden (one of the areas, near the Dutch city of Nimwegen), one harem roams separately from the large herd. This separate harem has its own territory, which is mainly located in the sub-area 'Oude Waal', which is connected to the rest of the area by a traversable dyke. During high tide, the Waal River forces this harem to move to Groenlanden, on the land side of the dyke, but the harem remains separate from the other harems in Groenlanden.

Two other areas do not contain a single large group, and they each have two harems with one dominant stallion each. In both areas, the dominant stallions have subdivided the area into two exclusive home ranges separated by a clear boundary. In one case, this is a narrow road crossing that divides the area into two parts. The other case concerns a long and narrow nature area with a limited contact zone separating both home ranges. In this last area, once during a dry summer, there was no more drinking water in one home range, forcing the local harem to travel to the other harem's home range to drink — after drinking, they would quickly leave 'enemy territory', each time, and return to their side of the

contact zone. Immediately after the rains had replenished the drinking water supply, the two home ranges returned to being occupied exclusively by their original harem.

Social groups within herds

The FREE Nature herds of free-roaming koniks in the Netherlands have a social organisation consisting of harems and bachelor groups. In 2013, there were 37 harems divided over 15 territories. In nine of these territories, there was also a band of stallions. In six of those, the bachelor groups roamed separately from the harems, whereas in the other three, they moved together with the herd.

FREE Nature area managers, on occasion, have observed groups of adolescents containing a young mare and some young stallions, but such groups are usually only temporary and a prelude to the formation of a new harem. Sometimes, sexually mature daughters remain in the harem into which they were born, but are serviced only by unrelated stallions. Illustrative in this respect is the following observation: 'This morning, there was some unrest in the herd. A closer look revealed that a yearling filly was outside the herd. She was being chased by the dominant stallion of her birth harem and then went over to another harem. Once there, she was serviced by a yearling colt. The dominant stallion of that harem stood by without interfering. Afterwards, the filly returned to her birth harem and peace was restored.' Some days later, she moved to the other harem, permanently.

In 2013, on four separate occasions, this occurred with a stallion from outside the harem. On one occasion, the dominant stallion did service his own daughter. Sometimes sons of dominant stallions service such daughters. This behaviour was not observed in 2013, but it did occur in 2014. Furthermore, not all adult mares within a harem allow the dominant stallion to service them. Of the 70 foals studied in the spring of 2014, 83% had been sired by the dominant stallion and another 9% by a stallion from outside the harem. The remaining 9% had been sired by adult stallions from within the harem. In two cases (3%), this concerned an adult son of the dominant stallion.

Subordinate stallions

In FREE Nature's herds of free-roaming koniks, similar numbers of colts and fillies are born (the gender ratio was 0.93 in 2013, with 53 colts against 57 fillies). In the herds in total, however, the gender ratio is less balanced, varying from 0.73 (1 January 2013) to 0.62 (on 31 December 2013).

In 2013, 46% of all FREE Nature harems contained more than one adult stallion, but only one dominant stallion per harem. The other stallions were found to be subordinate stallions, in a subservient, supportive role. Usually, there would only be one subordinate stallion, but in 8% of cases there were two or three. In territories with fewer than 25 horses in total, 18% of the harems have a subordinate stallion, whereas in those with more than 25 horses per area, this is 58%. Moreover, in the latter category, harems more often have more than one subordinate stallion (20% in large herds, against 0% in small herds).

Harems with more than one dominant stallion are rare in FREE Nature herds. Only one such case is known, in the Rug nature reserve, near Roosteren, along the Meuse in the province of Limburg, but this situation was not present in the year 2013. Both of those stallions originated from the same bachelor group. Another known case is that of a three-year-old stallion and a four-year-old stallion from the same bachelor group, who together succeeded in conquering a harem. Surprisingly enough, the youngest of the two went on to become the dominant stallion, and the older, subordinate stallion has not serviced any mares in years.

The herd at the Oostvaardersplassen

At the Oostvaardersplassen, which is a nature area rich in food, around 1150 koniks live in

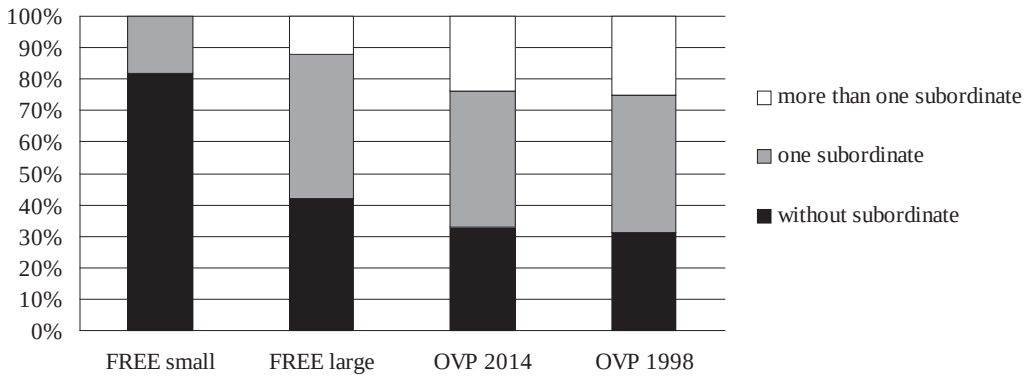

Figure 1. Percentage of subordinate stallions in harems of koniks; in areas (1) with a small FREE Nature herd (summer 2013, *n*=11) and (2) a large FREE Nature herd (summer 2013, *n*=26), and at the Oostvaardersplassen (3) in the autumn of 2014 (*n*=58) and (4) the spring of 1998 (*n*=32).

one large herd, in a more or less balanced gender ratio, on 24 km^2 of short and tall grasslands with patches of young forest. This equals a population density of around 48 horses per km^2. In 1998, the herd was much smaller, 391 horses, and consisted of 32 harems, each with one dominant stallion and 3.6 mares, on average. In 2014, there were 58 harems in the part of the herd that we counted.

Subordinate stallions

Similar to the FREE Nature herds, the harems at the Oostvaardersplassen also contain many subordinate stallions. In both 1998 and 2014, 67% of harems had at least one subordinate stallion. In both years, 25% had more than one subordinate, with a maximum of six adult stallions in one harem in 2014 (in 1998, the maximum was eight). Harems with only one adult stallion, thus, are in the minority, and were found to roam along the edge of the herd more often than those with multiple stallions.

Figure 1 shows that subordinates are found in over half of all harems — in large FREE Nature herds and those at the Oostvaardersplassen. In FREE Nature areas with small herds of koniks (fewer than 25 individuals per herd), subordinates were observed in 18% of harems.

Subordinate stallions not only occur regularly in konik harems, they also constitute a sizeable share of the herd. Of the 509 horses counted in the harems at the Oostvaardersplassen in 2014, 11% were dominant stallions and 12% were subordinate stallions. The harems studied, on average, each consisted of nine horses, which were dominant and subordinate stallions, mares and those too young to live outside their harem of birth. Only few bachelor groups were seen, and they were always found to consist of young stallions only. In addition, solitary stallions were observed, as well.

During the study of 1998, dominant stallions made up 11% of horses living in harems and 16% were subordinate stallions (figure 2). The harems consisted of an average of nine animals per harem, including two foals. Of all male animals older than one year, nearly half were either dominant stallions or subordinate stallions in a harem; here, also, there were more subordinate stallions than dominant ones, with 19% and 28%, respectively (of those over the age of one). Nineteen per cent of young stallions (between one and three years old) were in a harem, and only 9% were in a bachelor group. The remaining stallions (25%) were living a solitary life. Harems, on average, had three adult mares for every two adult stallions. The gender ratio of the entire herd was 1.01 (167 stallions against 165 mares).

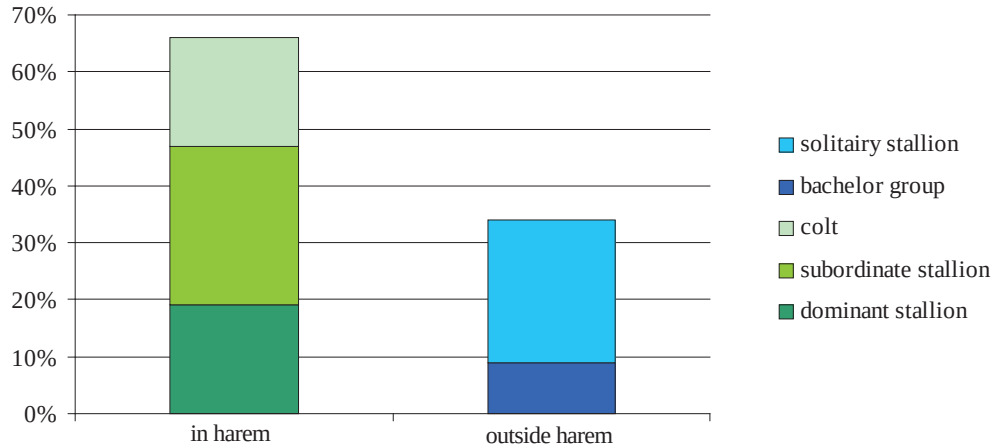

Figure 2. The number of stallions over the age of one, at the Oostvaardersplassen in 1998, outside and in harems, distributed over the various social categories.

Discussion

Habitat conditions

Exclusive home ranges are rare among feral horses, who mostly live in overlapping home ranges (Berger 1986, Linklater 2000). They are also rare among the FREE Nature koniks. A narrow connection between two nature areas does invite the forming of two exclusive home ranges. Two nature areas in which home ranges were exclusive, indeed had such a narrow part (see above) separating them. The third case concerned a long and narrow nature area. In the three areas, the contact zone between the exclusive home ranges was only small, which also made the ranges easier to defend. Moreover, these nature areas all had an ample supply of food and water, and primary needs are usually no impediment to the forming of an exclusive home range. This is similar to the situation on Canada's Shackleford Island (Rubenstein 1981), where three exclusive home ranges are located on the narrow part of the island, which has an amply supply of food and water and boundaries between the home ranges are relatively short. On Shackleford Island, the sea takes care of the 'defence' of the other boundaries, whereas the areas with herd from FREE Nature have cattle grids around them. However, in these three cases, the areas were not really territories, as instead of the boundary, the harem was actively defended (Linklater 2000). Therefore the herds of FREE Nature also have no territories but exclusive home ranges that result from spatial conditions and are not characteristic of feral horses (Linklater 2000).

In most of FREE Nature areas with large herds of koniks, all animals roam together as one group that consists of several harems, bachelor groups with young stallions and solitary stallions. This behaviour is not out of necessity, as food and water are plentiful throughout these areas (contra Linklater 2000). Such large herds of horses have also been observed elsewhere (e.g. Berger 1986).

In the small FREE Nature areas, bachelor groups often do live separately from the harem, as the dominant stallion has plenty of time to fend off the other, mostly young, stallions. Dominant stallions in these areas regularly go over to the bachelor group to posture and fight; confrontations that are always won by the dominant stallion, thus confirming his dominance. In places with multiple harems, a dominant stallion cannot abandon his harem for long periods of time because of the dominant stallions of other harems nearby. In such cases, a bachelor group will stay on the edge

Part of a large koniks herd at the Oostvaardersplassen, showing several harems. *Photo: Leo Linnartz.*

of the herd. This type of behaviour was also observed at the Oostvaardersplassen in 1998 and 2014.

The fierceness of the dominant stallions of harems as well as the season also partly determine whether bachelor groups are tolerated nearby. When mares are in heat, harem stallions are fiercer, and the young stallions of the bachelor group will stay at a greater distance from the harem, whereas older stallions of a bachelor group will in fact move closer to the harem's mares.

In contrast to plains zebras, dominant konik stallions do not work together to fend off bachelor groups. The konik stallions in such groups are mostly inexperienced and usually do not collaborate, which means there is no need for the dominant stallions to work together.

In the FREE Nature herds of koniks, there is little competition over food. Adult mares foal every year, and up to an advanced age, and there are hardly any winter deaths. This means an average annual 30% increase in the herd (2008–2014 period). The fact that the large herd of over 1000 koniks at the Oostvaardersplassen breaks up into several sub-groups in winter, when food is scarce, is an indication that the available food supply does play a role. An example, in this respect, is what occurred when a FREE Nature harem with a dominant stallion and one subordinate stallion was moved from food-rich Leeuwense Waard along the Waal River to the arid dunes of Oranjezon. In this area, which is low in food, the group rather quickly split up into two harems. There was not enough food for them to roam the area as one group, and the threat of rivals had ceased to exist. The dominant stallion and the subordinate stallion each took part of the harem for themselves and proceeded to avoid each other, although their territories did overlap.

The fact that food availability does play a role in herds splitting up does not explain the opposite; why they roam together in one group in times of abundance. Stallions and mares have different individual interests in group formation (Linklater & Cameron 2000). For dominant stallions, being far away from any rivals is appealing, whereas mares and their foals are vulnerable to predation and benefit from living in a large herd. This benefit disappears if, in winter, a dwindling food supply becomes a problem, and large herds are forced to break up into smaller ones. Thus, food availability does appear to be a limiting factor to the formation of large herds. Whenever the food supply is ample, large conglomerations of groups are formed. Plains zebras also form

large groups in such situations, with the largest herds being formed in locations where the competition from bachelor stallions is strong (Rubenstein 2011).

Another advantage of such large conglomerations which has not been mentioned before is that it enables the horses to dominate over other grazers. Whenever a large herd of koniks suddenly arrives in a certain area, free-roaming bovines or red deer (*Cervus elaphus*) move away. This happens not only at the Oostvaardersplassen, where around 1000 koniks live in a single herd, but also in FREE Nature areas with large herds. This provides the horses with access to the best grazing areas. Foraging opportunities and food supply therefore also determine whether free-roaming horses benefit from forming large herds.

Social organisation

In contrast to the herd at the Oostvaardersplassen, the FREE Nature herds are affected by human interference. At regular intervals, FREE Nature reduces the number of animals within a herd by rounding them up and removing a number of them. The social organisation of the herd is taken into account, as much as possible, by preferably removing complete harems or bachelor groups. Sometimes, young animals who are getting ready to leave the harem are removed as well. This practice appears successful, as the FREE Nature herds of more than 25 animals showed little difference with those at the Oostvaardersplassen, in both 1998 and 2014, in terms of harem composition and the occurrence of bachelor groups. However, there were fewer harems with more than one subordinate stallion in relatively large herds. In an entirely natural herd with an ample food supply, the age and gender ratios may be expected to be similar to those at the Oostvaardersplassen. In addition, there seems to be a gradient; a gradual increase in the number of subordinate stallions in growing herds, while there are hardly any subordinate stallions in small herds. The large herd at the Oostvaardersplassen was found to contain not only more harems with a subordinate stallion, but also, and particularly, a larger number of harems with more than one subordinate stallion.

Notable is the skewed gender ratio in the FREE Nature herds (0.73 and 0.62 versus 1.01 at the Oostvaardersplassen). This is primarily caused by human intervention. At birth, the gender ratio is far less skewed (range of 0.72–1.08, average 0.89, over the 2010–2014 period, with a total of 275 fillies and 246 colts). Moreover, the number of natural deaths among mares was observed to be higher than among stallions (13 and 3, respectively), whereas among the animals that were removed, stallions dominated (112 stallions versus 91 mares). Area managers are more inclined to remove a number of young stallions rather than an entire harem when a herd needs thinning to prevent the area from becoming overpopulated. In addition, bachelor groups are not always possible in smaller areas, when the dominant stallion will not tolerate them, or because the band avoids fighting the dominant stallion by moving out of the area, which means that area managers then need to capture and return them.

The social organisation of the large herd of koniks at the Oostvaardersplassen appeared not to have changed much in 16 years. This despite the fact that: 1. Numerous adult animals of the 1998 herd would no longer have been alive in 2014. 2. The herd nearly tripled in size since 1998, and 3. The conditions in the area had become more difficult, as the grazer population reached the area's carrying capacity already many years before. This indicates that the social organisation, as seen in 1998, is stable and typical for this area.

The situation of 1998, at the Oostvaardersplassen, shows that close to 20% of the stallions are dominant stallions and that harems also have a similar number of young stallions. Only 9% of stallions live in a bachelor group.

The others are subordinate stallions (28%) or solitary stallions (25%) that live among the herd. The same can be seen within the FREE Nature herds, despite the skewed gender ratio. Only a small number of stallions managed to become dominant stallions; some were too young and lived in a harem or bachelor group where they were learning how to fight, thus increasing their chances of one day conquering a harem for themselves; others were solitary or subordinate stallions. Wild horses that live in New Zealand and North America show a similar picture (Linklater 1998, Berger 1986), despite the fact that those animals do not live in large herds and do have overlapping territories.

Some of the harems with multiple stallions at the Oostvaardersplassen may have two stallions in equal position who came from the bachelor group at the same time and, together, conquered the mares (Rubenstein 2011, Ransom & Kaczensky 2016). The FREE Nature herds, however, hardly show any of such coalitions. In general, the stallions have clearly distinct roles; the subordinate stallion fights off any intruders and the dominant stallion stays with his mares. This division of roles is also often seen at the Oostvaardersplassen, and in 1998 no harems were observed with stallions in equal position (Nieuwdorp 1998). Most of the harems' additional stallions counted in 2014 would have been in a subordinate position. The horses benefit from a clear division of roles, as this keeps the number of conflicts to a minimum - which in turn benefits the mares, as it increases their opportunities for nursing their foals, and thus also reduces foal mortality.

Subordinate stallions compared

Subordinate stallions are common in the large FREE Nature herds and at the Oostvaardersplassen (figure 1), with 58% to 69% of harems having one or more subordinate stallions. This is a higher percentage than reported for herds elsewhere (by up to 50% (Linklater 2000)). The maximum number of subordinate stallions per harem is also higher at the Oostvaardersplassen than in harems elsewhere, with a maximum of eight at the Oostvaardersplassen versus four elsewhere (Linklater 2000). In nature areas with large herds of koniks, there is a large degree of rivalry between adult stallions. Particularly in the period after foals are born and mares come in heat again, stallions fight frequently and barely allow themselves time to eat. Bachelor stallions will attempt to service a mare in heat, or to conquer her to start a harem for themselves. And then there are the dominant stallions of other harems, who try to conquer a mare to add to their own harem. This applies not only to rivalling harem stallions, but also to solitary, adult stallions and the more mature stallions in a bachelor band. In such cases, having one or more subordinate stallions in the harem is to the advantage of the dominant stallion, as they help him protect the harem.

The fact that there are fewer or no competing stallions in the smaller FREE Nature herds may be the reason why those herds have fewer subordinate stallions than the larger FREE Nature herds. And this would also explain why the enormous herd at the Oostvaardersplassen, relatively speaking, has the highest number of subordinate stallions. At the Oostvaardersplassen, the harems with only one stallion are positioned more often along the edge of the herd, compared to those that have subordinate stallions. This seems to confirm that rivalry between stallions is a particularly strong driving force behind the phenomenon of subordinate stallions. Studies of feral horses in North America also point to this fact; there are hardly any subordinate stallions among the low numbers of stallions on certain islands (Linklater & Cameron 2000, Ransom & Kaczensky 2016), whereas subordinate stallions are a common occurrence in herds with the usual 1:1 ratio between stallions and mares (Ransom & Kaczensky 2016).

Furthermore, in Latvia, subordinate stal-

lions appear to also help defend the harem against wolves. Following confrontations with such predators, harems were often found to have more subordinate stallions than they did before (J. van der Veen, personal communication). Bachelor plains zebras also have been observed to roam together in groups more often when the risk of predation increases (Rubenstein 2011). Mongolian wild asses regularly form large conglomerations of harems and bachelor groups, with stallions from various harems working together to fend off wolves (Feh et al. 2001). This may also explain the higher survival rate of foals in such large groups, compared to those in independent harems (Feh et al. 2001). Thus, dominant stallions appear to tolerate subordinate stallions more readily when doing so is to their advantage; a larger number of mares in a harem is likely to provide more offspring and, when the risk of predation is increased, the foal survival rate is higher with subordinates around.

Subordinate stallions may originate from various places; sometimes they are the sons of the dominant stallion. These sons often leave the harem again, at a certain point, to start their own harem. This also depends on a stallion's temperament. Most subordinate stallions, however, arrive from outside the harem, such as from a bachelor group. An unrelated subordinate stallion would be able to service the daughters of the dominant stallion, which saves them having to go outside the harem to be serviced by a stallion other than their farther. DNA data have shown this to happen on occasion, but not often. In 2013, for example, no such case was found, with subordinate stallions only having serviced adult mares in the harem, and not the dominant stallion's daughters. Research among mustangs in North America showed that, here too, the dominant stallion's daughters were hardly ever serviced by subordinate stallions or their father; they were mostly serviced by stallions from outside the harem (Berger 1986).

The possibilities for subordinate stallions to sire offspring within the harem are limited; in 2013, only four in 70 foals (6%) born in FREE Nature herds were found to have been sired by a subordinate stallion, while six were sired by stallions from outside the harem and two by sons of the dominant stallion. Subordinate stallions may have the opportunity to take over all or part of a harem, but this does not happen very often. Moreover, there is also a fair bit of aggression between the dominant stallion and subordinate stallions (also see Linklater & Cameron 2000). All things considered, their role as the subordinate stallion appears to have only few advantages for them. As is the case for feral horses in New Zealand, the free-roaming koniks also show no signs of mutualism or altruism (Linklater & Cameron 2000). Horses are typically social animals and it seems that subordinate stallions choose to join a harem and resign themselves to play the subordinate role, when and if the dominant stallion allows them to do so.

Furthermore, subordinate stallions and dominant stallions are also radically different in temperament. Subordinate stallions are fighters and hard workers, whereas dominant stallions are calm and caring. When subordinate stallions have the opportunity to act as dominant stallion, they are usually not very good at it. Their position is often taken over by a dominant stallion coming from outside, and they revert back to their subordinate role or are even chased off by the incoming dominant stallion.

In practice, there are large differences in temperament between dominant stallions as well (personal observations, T. de Bode & R. Meissner, personal communication). Some act very aggressively towards rivals, while others appear very caring towards the mares and foals. Ultimately, the mares choose their dominant stallion. If a stallion is not to their liking, he will not become the harem's dominant stallion (R. Meissner, personal communication). There have even been cases reported of mares themselves changing harem after the arrival of a new dominant stallion (T. de Bode, personal communication).

Conclusions

In contrast to elsewhere in the world, the free-roaming koniks in Europe mostly live in nature areas that are rich in food and have an ample supply of drinking water. Koniks appear to prefer living in large groups, which is accommodated by the ample, high quality food supply in the investigated areas. In two areas that were less rich in food, the harems opted to roam independently, and in winter, when food is scarce, large herds were also found to break up into smaller groups.

Exclusive home ranges containing a single harem were found in certain areas with narrow road crossings or dykes, or in long and narrow areas, but these are relatively rare. These home ranges are different from true territories, as only the harems were defended, rather than the land itself. Thus, independent harems or groups can be formed not only as a result of food scarcity but also because of the type of terrain.

Free-roaming koniks, in Europe, live in herds with a social organisation of harems and bachelor groups that is similar to elsewhere in the world among wild Equidae and feral horses. This contributes to the notion that past domestication is unlikely to have influenced the type of social organisation (Linklater 2000). In Europe, however, this organisation can only be observed in nature areas with larger herds that live in an autonomously chosen social structure — thus, in areas where there is only limited human intervention.

Having rivalling harem stallions and bachelor stallions looming nearby, however, is an inherent aspect of large herds. This is why harems in such large herds often have a particular composition that also includes subordinate stallions who play an important role, in addition to the dominant stallion, both qualitatively, in tasks, and quantitatively, in numbers. Such subordinate stallions also help to defend the harem against predation, and their numbers increase with the risk of predation. Subordinate stallions themselves, however, experience only few advantages in relation to their efforts. They hardly service any mares in the harem, and, if the dominant stallion should die, they do not often appear successful in holding on to the harem for themselves. Thus, among the free-roaming koniks studied, there appeared to be no mutualism or altruism. Subordinate stallions that join a harem were found to have a different temperament or develop in a different way, compared to dominant stallions.

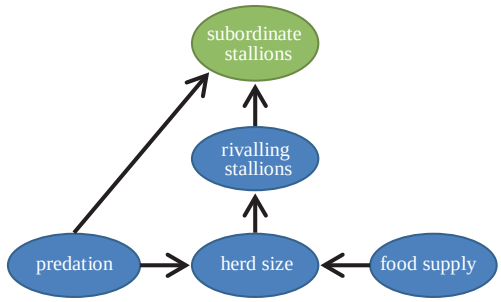

Figure 3. Predation and food supply determine herd size; herd size has an effect on the degree of rivalry between stallions; this rivalry, together with predation, in turn affects the number of subordinate stallions within harems.

In addition, predation also appears to lead to the formation of large groups as well as to more collaboration between stallions, although this is not (yet) the case in the Dutch situation. Subordinate stallions, therefore, are the rule rather than the exception, and their occurrence depends on herd size, the presence of rivalling stallions, predation and food supply (figure 3).

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Samenvatting

De sociale structuur in natuurlijke kuddes koniks (*Equus caballus*): secondanten, regel of uitzondering?

Dit artikel beschrijft de sociale structuur van kuddes vrijlevende koniks in Nederland en elders in Europa met bijzondere aandacht voor de Oostvaardersplassen. Daarbij richt onze aandacht zich op: 1. De grootte van kuddes in relatie tot de leefomstandigheden. 2. De samenstelling van de harems als onderdelen van die kuddes. 3. De relatieve aantallen en de rol van secondanten in die harems. Op basis van deze informatie schetsen wij vervolgens een beeld van de gedachte situatie rond secondanten in de Oostvaardersplassen en andere gebieden met grotere kuddes vrijlevende paarden. Daarna onderzoeken we de geldigheid van dit beeld voor andere gebieden in Nederland waar kuddes koniks grazen. Dat doen

we aan de hand van verzamelde veldgegevens waarbij ook de uitkomsten van een herhaling van het onderzoek in de Oostvaardersplassen worden betrokken. Tenslotte gaan we na of de verkregen uitkomsten ook van toepassing zijn op verwilderde paarden (*Equus caballus*), przewalskipaarden (*Equus przewalskii*) en zebra's, ezels en halfezels (*Equus* spp.) elders in de wereld.

Anders dan elders op de wereld leven vrijlevende koniks in Europa veelal in voedselrijke natuurgebieden met een ruime beschikbaarheid van water. Koniks blijken daar een voorkeur te hebben om in grote groepen te leven. Het goede voedselaanbod in de onderzochte terreinen ondersteunt het leven in grote kuddes. In een tweetal minder voedselrijke gebieden kozen de harems ervoor om ieder apart te leven. Ook als in de winter het voedsel schaars wordt, breken grote kuddes vaak op in kleinere.

In een aantal terreinen met een smalle weg- of dijkovergang of met een smalle, langgerekte vorm was er sprake van exclusieve leefgebieden van op zijn minst één van de harems. Dit waren geen territoria, omdat niet het leefgebied zelf, maar de harem werd verdedigd. Naast voedselschaarste kunnen dus ook terreinomstandigheden leiden tot het leven in gescheiden groepen.

Vrijlevende koniks in Europa leven in kuddes met een sociale structuur met harems en hengstengroepen die overeenkomt met de structuur zoals die wereldwijd voorkomt bij wilde paardachtigen en vrijlevende paarden. In Europa is deze structuur echter alleen waar te nemen in natuurgebieden met grotere kuddes in zelfgekozen sociale verbanden. Dus in gebieden waar menselijk ingrijpen beperkt is.

De aanwezigheid van meerdere harems maakt het echter wel noodzakelijk dat leidhengsten voortdurend concurrentie op afstand moeten houden. Harems in deze grote groepen kennen mede daarom vaak een aangepaste haremsamenstelling, waarbij naast een leidhengst ook secondanten een belangrijke rol spelen, zowel in taken als in aantallen. Onder dergelijke omstandigheden biedt de aanwezigheid van secondanten voordelen: ze helpen mee de harem te verdedigen en zorgen daarmee voor de broodnodige rust voor merries en hun veulens. Ook helpen secondanten mee om predatie te voorkomen en zijn er meer secondanten in situaties met predatiedruk. Secondanten hebben zelf echter weinig voordeel bij hun inzet. Er is bij de onderzochte vrijlevende koniks dus geen sprake van mutualisme of wederkerig altruïsme. Secondanten blijken wel een ander karakter te hebben dan leidhengsten.

Predatie blijkt ook te leiden tot het vormen van grote groepen en tot meer samenwerking tussen hengsten, maar dat doet zich in Nederlandse situatie (nog) niet voor. Het voorkomen van secondanten is dus eerder regel dan uitzondering en lijkt een relatie te hebben met, kuddegrootte, rivaliserende hengsten, predatie en voedselaanbod.

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