Final Report

LEADERSHIP IN PRZEWALSKI HORSES
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1. Introduction

Multilevel societies are among the most complex forms of social organization in nature. Studying them can contribute with a fundamental knowledge to the understanding of the evolution of sociality. Individuals in a multilevel society aggregate through multiple nested social levels. They form highly cohesive core units (e.g. one-male-multifemale units) which aggregate into less consistent larger groups within the population. It appears in a small subset of species, including some of the equids, cetaceans, and primates. Furthermore, the majority of human social systems shows the same multi-levelled structure. Thus, studying leadership and collective phenomena in a multilevel society may help to understand these processes in our own species, as well.

The aim of this project was to investigate leadership processes in Przewalski's horses (*Equus ferus przewalskii*), in the Hortobágy National Park (HNP), where the world's largest captive population of this species, counting almost 300 individuals, lives. Przewalski's horses, the last extant subspecies of wild horses, live in a multilevel society, in this reserve. Similarly to many other equids, Przewalski's horses live in long-term stable harems, including one breeding male - the so-called harem stallion -, several breeding females, and their young offspring, not yet dispersed. Non-breeding males form bachelor groups. Harems and bachelor groups in the HNP's reserve aggregate into a large herd, and the whole population synchronizes their movement and behaviour, all year round.

In this project we also aimed to use state-of-the-art observational methods in the field of behavioural ecology, and experiment with new solutions in the observations of wild populations. As we proceeded with the project, we succeeded to develop an observational method, based on multiple drones, that made it possible to investigate not only some focus harems, one-by-one, as it was proposed originally in the workplan, but we could record the collective movements of the whole population of the reserve, while ensuring individual identification for most of the horses. Hence, we decided to partially modify the project plan, and to investigate the collective movements and leadership in the whole population, a multilevel society of wild horses. The first results made it clear that many aspects of the horses' society are reflected in their group movements, thus we focused first on revealing the structure and functioning of the society.

2. Observations

During the research project we have made several observations of the collective movements and social behaviour of Przewalski's horses in HNP. We performed field observations with a state-of-the-art method, we used drones to track the movements of the free-ranging animals.

We observed the herd's movements with multiple drones, a higher drone recorded a top view video for tracking the individuals, while a lower drone scanned through the horses to get a detailed

view for individual identification (Figure 1A). Trajectories of individuals were calculated in an earth-fixed coordinate system, with high temporal and spatial resolution, while most of the horses were individually identified (n = 238 identified and 40 unidentified individuals, Figure 1B-C). With this multiple-drone method we observed the herd in two contexts, (i) during movements, when as a part of their daily routine the horses walked between feeding and drinking places, and (ii) while the horses were resting.

To investigate social behaviour (social bonds and social dominance) of individuals we recorded some harems by a single drone during feeding, since most of the aggressive behaviour occurs in this context. In this type of observations, it was necessary to see the body-language of individuals in detail, thus we recorded the harems from close-up, and one-by-one (like Figure 1A – Drone 2 view). The half of the harems was included in this observation (in total 16 harems was included from the existing 31 harems).

The HNP's wild horse population lives under semi-natural conditions, mate choices and group forming are not inferred by humans. Since the founding of the reserve in 1997, all individuals of the population are individually identified and monitored, the latter includes the recording of individuals' life history, DNA-based parentage data and changes in harem compositions. In the frame of the project, we processed the data of this 20+ years of population monitoring and organized it into a unified database, because we aimed to use it in combination with the short-term drone-recorded movement observations (Figure 1D). Some results, partially related to this project, thanks to the database organization are published in [P1].

3. Results

3.1. Collective movements reflect structure and dynamics of multilevel society in Przewalski's horses

Although several attributes of multilevel societies are well known, the relationship between individual behaviour and society structure is not fully understood. To explore how the structure and dynamics of a multilevel society is reflected in the population's collective movements, we observed the fine-scale movements of almost 300 free-ranging Przewalski's horses, and combined this observation with decades of population monitoring. We filmed short-term movements with drones, and tracked all individuals' movement on the aerial videos in high temporal and spatial resolution (Figure 1B). Most of the horses were individually identified (n = 238) and their identities were matched through the observations on different days. We analysed the individual movement trajectories, and calculated pairwise movement interactions, to study whether the herd's spatial structure and movement is affected by kinship, social levels and past experiences of individuals in the society.

We observed that although the whole herd moves very coherently, different levels of cohesion is characteristic of the different social levels. This finding makes it possible to distinguish the sub-units (harems and bachelor groups) inside the herd based solely on their movements, observed through several minutes. Analysis of movement interactions between the individuals revealed a social network of the herd (Figure 2). We investigated the relationship of this network with the kinship of individuals, and the history the individuals share as former harem mates. We found that inside the harems the individuals are closer to each other in the network, if they are closely related (i.e. parent-offspring or sibling relation) or have a long shared history as former harem mates. Proximity on the social network also means spatial proximity and higher similarity of movement.

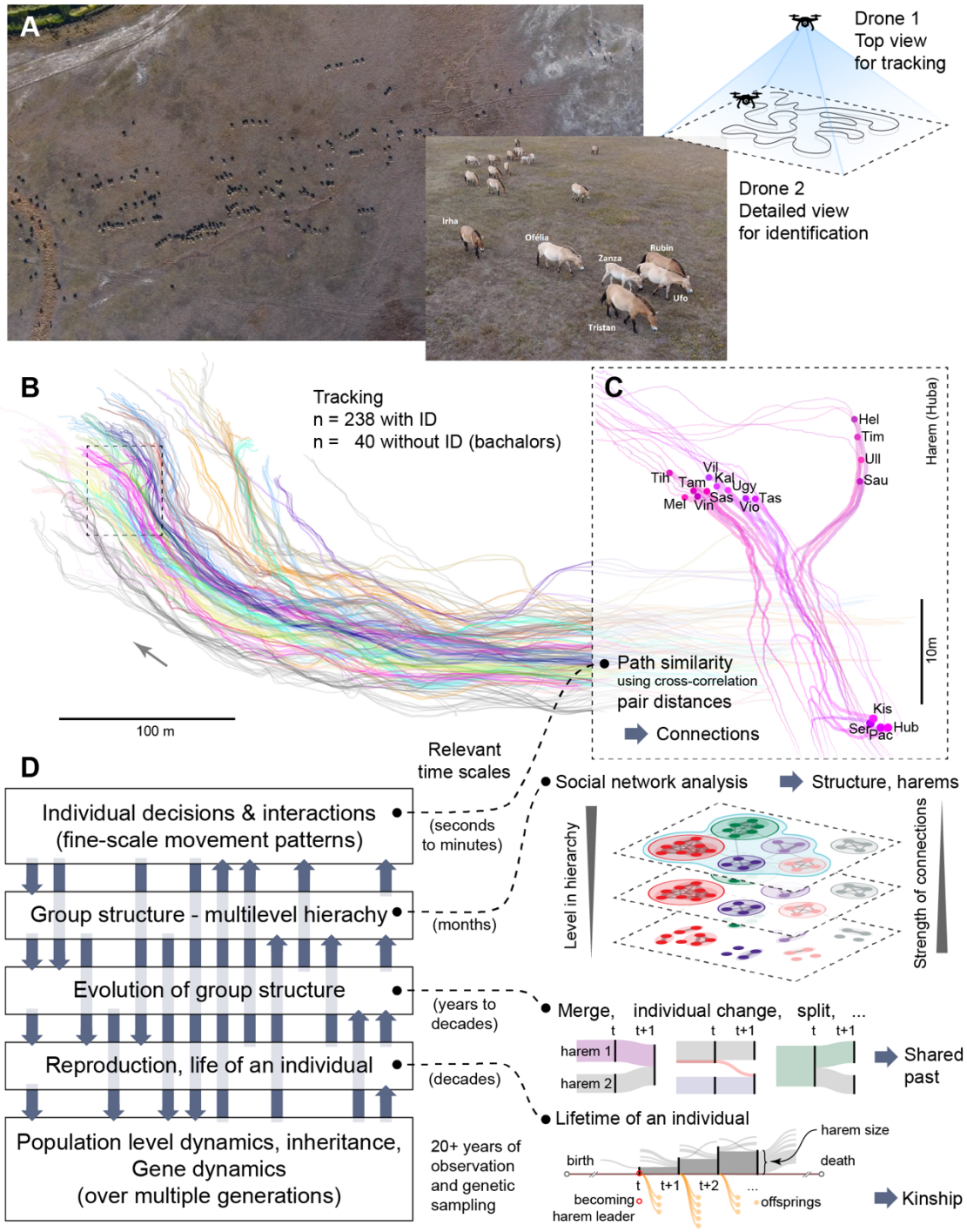

Figure 1. Overview of the main concept and the data aquisition techniques. A Sample images and a sketch of the setup for high resolution filming of wild horses with multiple drones. The higher drone provides a large-scale top view for tracking individuals (and the background) to get movement coordinates in an earth-fixed coordinate system (B). The lower drone scans the area with horses to get a detailed view for individual recognition. **B** Example trajectories of all horses belonging to the population from a 5-minutes long recording. Arrow shows the main direction of motion. Individuals (recognized ID) are color-coded based on the group (harem) they belong to, or with grey in case of bachelors. **C** Detailed view of trajectories of a single harem, with all individuals shown with dots at a given point in time. Three letter IDs show their identities. **D** Diagram of the main concept (on the left) showing important aspects of collectively living animals, and how complex interplay between these components affects each other. These components may have a relevant temporal scale (shown in the middle) that spans through several orders of magnitudes (from seconds and minutes to several decades). A detailed schematic explanation (on the right) of each component.

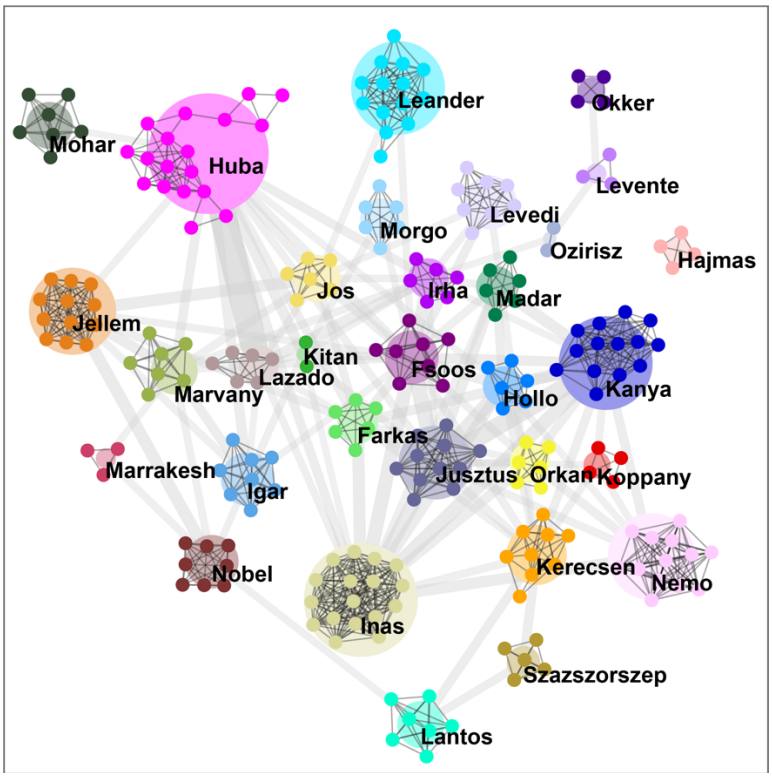

Figure 2. Social network of the herd. Nodes correspond to individuals of the population, while colours denote the harems they belong to. An edge is drawn between two individuals (harems) if their average distance through the observations is lower than a threshold. All individuals of HNP included, except bachelor males.

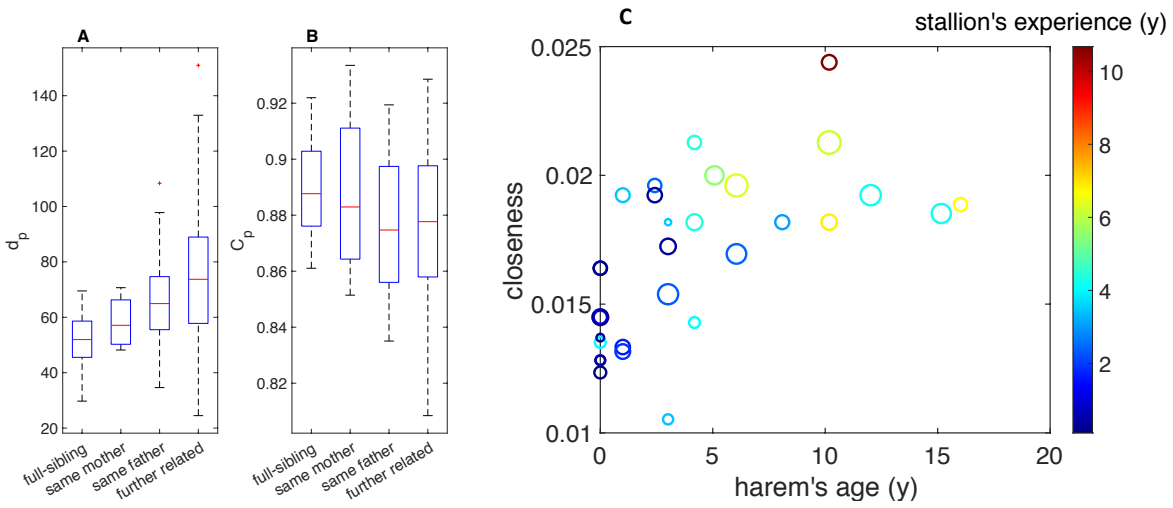

Figure 3. A-B Distance (A) and movement similarity (B) of harems is in connection with the kinship of their stallions. **C** Closeness centrality of harems in the network (Figure 2) against the harem's age in years. Node size denotes the total size of the harems, while node colour the harem stallion's experience in keeping a harem.

Analysis of the harem network showed that harem aggregation is also based on kinship and shared history between the individuals, and the harems are connected also by female-female, and male-male bonds. Harems of related stallions (siblings and half siblings) are located closer to each other in the network (Figure 3A-B). Additionally, if we consider the migration of breeding females

between the harems, we find that female transfer is more frequent between the harems closer in the network, both in the two years prior to, and both in the two years following the observation. The centrality of the harems in this network is related to the harem's age, harem's size and the stallion's harem keeping experience (i.e. the time during the stallion owned a harem). Older and larger harems, led by a more experienced stallion are more central, while younger, smaller harems led by a less experienced stallion are more peripherical (Figure 3C). Since bachelor groups are observed on the periphery of the herd, the structure of the harem network suggests that the aggregation of harems into herds may be mainly driven by a collective defence strategy by the harem stallions, against bachelor threat and infanticide.

Movement similarity of the adult females can also predict their future harem changes. Females currently being members of different harems move more similarly, if they will be harem mates in the next two years, at least for half year. Similar effect was found inside the harems, the females that are currently harem mates, move more similarly if they will stay harem mates for at least half a year. In this way, movement interactions can predict future changes in the society.

We found that fine-scale movement interactions are related to the structure of the society, and even a short recording of several minutes duration reflects social processes occurring over years, both in the past and in the future. Hence, studying delicate interactions can give insights into the possible origin and function of a multilevel society. These results are detailed in a preprint [P2].

3.2. Leadership during collective movements in the multilevel society of Przewalski's horses

Leadership is an important phenomenon in nature, although it was not yet described in a multilevel society. We investigated the leadership during collective movements in a multilevel herd of Przewalski's horses. We tracked all individuals' trajectories on drone-recorded videos, and quantified the leader-follower relationships by calculating the directional correlation delay between the pairs of individuals. The directional correlation delay method identifies similar path segments, and quantifies the temporal relationship of the individuals' changes in movement direction. We found that leadership is related to individuals' position within the group. Considering the front/back axis of the harem, leaders walked ahead of the harems. Similar leadership pattern was found inside the whole herd, leader harems walked ahead of the herd. For this reason, we refer to individuals (and harems) walking in the front as leaders, and the others walking behind as followers. We found that leadership roles of individuals inside the harems are consistent over time, and are related to the status (i.e. adult female, juvenile, harem stallion) and age of the individuals. Leaders are mainly adult females, while juveniles and harem stallions tend to be followers. An age dependence was found both in females and males, older individuals are more leader-types. Besides the movement observations, we performed classical behavioural observations of focus harems, when social interactions between individuals (aggressive and friendly) were recorded on close-up drone videos. Based on different dominance measures (David's score, proportion of won and proportion of initialized aggressive interactions), the leadership ranking inside the harems seems to be independent of dominance ranking.

In contrast to the consistent leadership order inside the harems, we did not find a leadership order, consistent over time, among the harems. On different observation days it was highly variable which harems became leaders of the herd. It is an interesting and unexpected result, that leadership works differently in the different levels of the society (i.e. in harems and in herd). This topic needs more analysis to be clarified. Based on these results a manuscript is in preparation [P3].

4. Ongoing studies

In the frame of this project, we collected a huge amount of observational data, mainly in the form of aerial videos. Many of them are already processed, also the first results are obtained, and we continue to analyse them in the following years. The main topics, in which we made significant advances, are introduced below.

4.1. Long-term study of leadership

We performed the same movement observation of the whole population (cca. 280 individuals) in two consecutive years (2018/2019), in the same season. Between the two observation seasons, some of the harems have split, some new emerged, while others have changed in their composition, due to female transfer between the harems and juvenile dispersion. We aim to investigate the relationship between group dynamics and the changes in the leadership structure and collective movements. Trajectories and IDs of the individuals, needed for this study, are already reconstructed from the aerial videos.

4.2. Herd structure in different contexts

In 2019 we observed the herd in two contexts: during collective movements and while resting. The observations of the resting herd were carried out in a similar manner, than the movement observations: through several minutes all individuals of the population were tracked on aerial videos, while most of them are individually identified. The observations are already processed, trajectories and IDs are reconstructed. We aim to investigate the structure of the herd, centrality of the harems and bachelor groups, and also the proximity of individual pairs, and its relationship with kinship, shared history as former harem mates, and frequency of friendly interactions.

4.3. Social interactions

Social interactions between the individuals were observed on drone-recorded videos in 16 harems (in total n = 145 individuals, and 45 hours of observation), during the two observation years. All videos are processed. Interactions were coded based on a very detailed ethogram, and classified by cluster analysis into two main categories, which based on the main features were referred as aggressive and friendly. We found that aggressivity and friendliness are primarily related to the status of an individual in the harem, and aggressivity also to sex. Although, differences in individuals did not support yet the existence of different personality types, we found significant differences between the harems in the initiated frequency of aggressive interactions. We aim to further investigate personality traits, and whether they are related to leadership roles.

4.4. AI-aided detection and identification of individuals

Aerial videos captured by drones were processed manually during this project, and individual movement was tracked. This database, containing millions of coded individual positions on the videos, serves as an excellent training dataset for developing artificial intelligence (AI) aided solutions for automatic detection and tracking of individuals on aerial videos. We started to proceed in this direction, and our first results are promising, detection efficiency is over 90%, which already offers a quick and affordable method for population size estimation in remote areas. We aim to further work on solving the movement tracking of individuals, and the individual identification.

4.5. Coloration

Some phenotypic variables connected to fur colour and fur thickness (e.g. coloration of legs, colour of mane, intensity of shoulder cross, length of mane, etc. - 18 variables in total) were coded on the detailed-view drone videos (Figure 1A) for most of the population (n = 268 individuals). We aim to study whether fur coloration serves as signal, and is related to individual breeding success. Since the pedigree tree is known for the population, heritability of coloration can also be investigated.

4.6. Group dynamics

We built up a database, suitable for analyses, from the 20+ years long observation data of HNP on group dynamics. We plan to investigate harem development, and mate choice preferences of the females.

5. Differences from the project plan

The main difference between the project plan and the realized project is that the primary question of the research was partially modified, as it is explained in the Introduction.

Originally, we planned to observe the movements of 10 focus harems, filming the harems one-by-one, in summer seasons. During the project, we observed the whole population, counting 278 individuals, in total 31 harems and 10-12 bachelor groups. We also planned to observe 4 focus harems, monthly, through two years, to investigate long-term processes. Due to difficulties in winter seasons (limited access of the area in harsh weather conditions) this plan could not be carried out. Instead, we observed the whole population's movement in two consecutive years.

It became clear only during the project realization that we are able to observe the whole population, and individually identify all harem-living horses (n = 238), only the bachelor males were unidentified. Thus, we decided to study the collective movements of the whole population. This was an ambitious aim, that pointed far beyond the scope of the original project plan, and also offered an opportunity to deeper understand the processes, such as leading, in multilevel societies. Although, we did not count properly with the huge amount of time needed to process the aerial videos for this study, which significantly delayed the progress of the project and the publication of the results. We tracked the movements of each individual (n = 278), during 12 observation sessions, through 4000 coordinate points in each session, which means more than 10 million location points in total. The processing was made mainly manually, and each observation video had to be re-watched 278-times, to track each individual, separately. Although more students were involved in the video analysis, we succeeded to finish the evaluation of the observations only in the fourth year. Although delayed, but we could achieve valuable and unique results. Our manuscript on the relationship between fine-scale collective movements and the dynamics of the multilevel society is in online preprint format and close to submission.

6. Fund reallocations

During the project realization some slight changes occurred in the planned personal costs: (i) the employment of a project administrator was not necessary, (ii) due to the large amount of videos needed to be processed, increased costs arose in the employment and extra scholarship for students who participated in the video analysis, (iii) the employment of the leading researcher was extended, because the duration of the project itself was also extended after the approval of the NKFIH. Due to

accounting technical issues some accessories for drones were moved from “4. Invested assets” cost category to the “3.2. Supply purchasing” cost category.

7. Summary

During the four years of the grant period, we performed many observations, developed state-of-the-art methods, and made significant progress towards understanding processes, such as leadership, in multilevel societies. We also collected and processed a huge amount of data, which will provide a great basis for further studies in the following years. A number of students were involved into the project, participating in video processing and behavioural observations. Five of them have completed their BSc thesis and two students completed their MSc thesis successfully. We are grateful for the support of NKFIH.

8. Publications

8.1. Scientific papers

[P1] Kerekes V., Sándor I., Nagy D., Ozogány K., Göczi L., Ibler B., Széles L., Barta Z. (2021). Trends in demography, genetics, and social structure of Przewalski’s horses in the Hortobagy National Park, Hungary over the last 22 years, *Global Ecology and Conservation* 25, e01407 (doi:10.1016/j.gecco.2020.e01407)

8.2. Preprints

[P2] Ozogány K., Kerekes V., Fülöp A., Barta Z., Nagy M. (2022). Fine-scale collective movements reflect structure and dynamics of multilevel society in wild horses, soon to be submitted to *Nature Communications*

8.3. Manuscripts

[P3] Ozogány K., Kerekes V., Fülöp A., Barta Z., Nagy M. (2022). Leadership during collective movements in a multilevel society of wild horses, in preparation

8.4. Talks

Ozogány K., Kerekes V., Nagy M., Barta Z.: Movement patterns and leadership in a multilevel social group, ASAB 2019 Summer conference: New Frontiers in the Study of Animal Behaviour, Konstanz, Germany, 26-28 August 2019

Kerekes V., Ozogány K., Sándor I., Végvári Z., Czető C., Nyírő B., Szabados T., Széles L., Barta Z.: Habitat use, activity, and body condition scores of Przewalski’s horses in Hortobagy National Park, Hungary, VII International Symposium on the Preservation of the Przewalski Horse, Orenburg, Russia, 26-29 August 2019

Ozogány K., Nagy M., Kerekes V., Barta Z.: A hortobágyi Przewalski-lovak csoportos viselkedésének megfigyelése drónokkal, XXII. Conference of the Hungarian Ethological Society (online), 4-5 December 2020

Kerekes V., Sándor I., Ozogány K., Barta Z.: A Przewalski ló hortobágyi állományának változása az elmúlt 20 évben, XXII. Conference of the Hungarian Ethological Society (online), 4-5 December 2020

Barta A., Katona D., Ozogány K., Bán M., Kerekes V., Barta Z.: AI and wild horses, AI for Earth Digital Summit (online), 17-19 November 2020

8.5. Posters

Ozogány K., Kerekes V., Nagy M., Barta Z.: Movement patterns and leadership in a multilevel social group of Przewalski horses, International Wild Equid Conference, Prague, Czech Republic, 1-5 September 2019

8.6. Related papers

Kerekes V., Ozogány K., Sándor I., Végvári Z, Czető C., Nyírő B., Szabados T., Széles L., Barta Z. (2019): Analysis of habitat use, activity, and body condition scores of Przewalski's horses in Hortobagy National Park, Hungary (conference article), *Nature Conservation Research* 4 (Suppl.2): 31-40 (doi:10.24189/ncr.2019.029)