

# **Exploring the formation, maintenance, and adaptive significance of multi-male groups in feral horse societies**

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## **Introduction**

Animals adapt their behaviour to maximize their fitness in response to differences in their social and ecological environment, as well as competitive capabilities, so that we may expect variation in mating behaviour. In polygynous mammals, male's mating success is highly variably and therefore competition for mates is intense with only a few individuals achieving reproduction. Consequently, some males may employ alternative mating strategies. In feral horses (*Equus caballus*), females (mares) can associate in year-round social groups with one male (single-stallion (SS) groups) or multiple adult males (multi-stallion (MS) groups). However, as stallions compete to monopolize mares, MS groups raise questions regarding their formation, maintenance and adaptive value. This thesis aimed to provide new insights on stallion mating strategies by reassessing previously proposed hypotheses and exploring intra-specific variation in stallions' traits, using a multidisciplinary approach and non-invasive technologies. In *Chapter 2*, I explored if morphological features are a differentiating factor between stallions of SS and MS groups. In *Chapter 3*, I tested the costs and benefits predicted for MS groups by previous studies. In *Chapter 4*, I looked into patterns of stallion-mare and stallion-stallion socio-spatial behaviour in feral horses and their contributing social factors.

## **Methods**

Data was collected from a feral Garrano horse population in Northern Portugal. In *Chapter 2*, I used a non-invasive, laser distance meter to measure distance to target and determined individual body length and height by overlapping photos of individual horses and a measuring tape. I then tested the accuracy of remote measurements by manually and remotely measuring domestic horses. For *Chapters' 3 and 4*, I used the population's demography data over a six-year period (2016-2021) to analyse group size, stability and foaling rate of MS and SS groups. For behaviour analysis, I focused on a total of 14 SS groups and four MS groups, and the data collection period varied between the months of May and August (comprising the breeding and birthing season) from 2018 to 2020. I conducted daily 1-h focal group observations, representing a total of 314 h of observation (ranging from 6–40 h per group). Simultaneously, every five minutes I scanned the activity of focal group's members to compare feeding and resting time of SS and MS groups. Aerial photo scans were taken every 10 min to record the spatial behaviour of all individuals. Fecal samples from the whole population were collected to examine genetic relatedness between individuals and

determine stallions' reproductive success. Statistical analysis was mostly done with Mixed Models in R software.

## **Results & Discussion**

### *Chapter 2. Does size matter? Examining the possible mechanisms of multi-stallion groups in horse societies*

Body size did not vary significantly among stallions, regardless of their status or female group size, suggesting that body size is not a good indicator of male quality and/or fighting ability in horses, as observed in other polygynous species. Thus, the hypothesis that MS stallions are inferior competitors, based on their size, and consequently cooperate to enhance their reproductive opportunities was not supported. A highpoint of this study was the development and use of a non-invasive methodology to measure horses at a distance, with easy replicability and application to other species, without needing to resort to stressful handling of animals.

### *Chapter 3. Examining the costs and benefits of male-male associations in a group-living equid*

Contrary to mutualistic hypotheses, results indicated that SS stallions had more breeding mares than MS groups and group type did not influence mare membership stability. However, dominant stallions in MS groups may be benefitting from the presence of another stallion, via decreased effort in group defence and more resting time. I recorded less aggressive behaviours from dominant to subordinate stallions in MS groups when subordinates displayed more defensive behaviours against outsiders, but I found little evidence that subordinates were being rewarded with access to mares, as proposed by reciprocal-altruism hypotheses. Conversely, I did not find discernibly clear negative effects of stallion-to-mare harassment in MS groups as proposed by the Consort hypothesis. Additionally, this study was the first to report on predation impact by wolves in MS and SS groups, highlighting the need to further explore how different ecological pressures shape horse behaviour and social organization.

### *Chapter 4. Patterns of male-female and male-male association in a group-living equid*

Mare group size, rank, reproductive status, and genetic relatedness had a significant influence on stallion-mare distance. The frequency of affiliative interactions between the sexes was mainly affected by mare group size and reproductive status, while stallion aggression towards mares was driven by mare group size, tenure, and genetic relatedness. While MS dominant stallions and SS stallions displayed similar patterns of interaction with mares, I found insufficient evidence for close MS subordinate stallion-mare relationships from any metrics. Challenging prior hypotheses framing MS groups as competitive associations driven

by stallion-mare consort relationships, these findings suggest it is the bond between the stallions that contributes to subordinate maintenance in MS groups.

## **Conclusion**

Animal social interactions are nuanced, and cooperation and competition can be closely intertwined, even among cooperating male partners. Collectively, the data presented here seems more in favour of cooperation (or at least, very high tolerance) among stallions in MS groups, but I believe it also highlights how demography and social structure can account for much of the variation observed across different feral horse populations. I conclude by outlining several potential directions for future research, including aspects of stallions' traits and social environment that deserve further exploration. Here I present novel results and offer new insights on the topic of MS groups, which have application for domestic horses' welfare and population management. Ultimately, the findings of this thesis can contribute to our broader understanding of the selective pressures underlying alternative mating strategies and male sociality in polygynous species.