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Does size matter?

Examining the possible mechanisms of multi-stallion groups in horse societies

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Abstract

In some feral horse populations, adult females are either associated with a single male or multiple males (stallions). However, little is known on why such groups with more than one male exist, considering that stallions fight to monopolize females. Body size is often an important determinant of male fighting ability and/or dominance rank and, consequently, reproductive success. Stallions may, therefore, vary in “quality” which could be a differentiating factor between single-stallion and multi-stallion males. We observed feral Garrano horses in Northern Portugal and examined the relationship between body size, sex, group type and number of females. Using a non-invasive laser distance meter, we determined individual body length and height by overlapping photos of the horses and a measuring tape. We tested the accuracy of remote measurements by comparison with manually measuring domestic horses and found no statistical differences between the two methods. Thus, we assume the values obtained were reliable and the methodology used was a useful tool for assessing morphological characteristics. Results showed no significant differences in body length and height for all parameters assessed, suggesting that size is not a determinant factor for feral horse society. Thus, other factors may be more important to explain the existence of single and multi-stallion groups.

1. Introduction

In polygynous mating systems, males compete intensely for mating opportunities and, according to sexual selection theory, traits that grant an advantage during contests (i.e., fighting) are under high selection pressure (Andersson, 1994; Darwin, 1871). These traits can also result from female mate choice if females select mates that exhibit characteristics associated with individual quality (Andersson, 1994). In several taxa, male body size often positively correlates with fighting ability and/or dominance rank and, consequently, reproductive success (Alcock, 1996; McElligott et al., 2001; Modig, 1996; Wright et al., 2019). However, it is possible that individuals who find themselves at a disadvantage may work together to improve their prospects. Male sociality in the form of reproductive cooperation has been described in several species (Bygott et al., 1979; Chowdhury et al., 2015; Connor et al., 1992; Duffy et al., 2007) and occurs when two or more males, which would otherwise be reproductive competitors, join efforts to attract, gain, or maintain access to females. In rhesus macaques (*Macaca mulatta*), males that formed revolutionary coalitions had more similar features than other males, such as rank, body mass, and canine size, and worked together to overthrow the alpha male and shift the dominance hierarchy, consequently improving their reproductive opportunities (Maestriperi and Higham, 2010).

In the wild, horses (*Equus caballus*) form year-round social groups composed of at least one adult stallion, several unrelated mares, and their immature offspring. Although stallions fight to monopolize the females, multi-stallion groups live in sympatry with single-stallion groups. These groups are characterized by a strong hierarchical relationship among the males, where one stallion is clearly dominant over the others (Feh, 1999; Miller, 1981). The subordinate stallions may help with group defense and may occasionally be able to copulate with the mares (Feh, 1999). In the past, several hypotheses based on alternative mating strategies, such as male parasitism, by-product mutualism, and reciprocal altruism, were proposed to explain the existence of multi-stallion groups (Feh, 1999; Miller 1981; Stevens, 1990). However, Linklater and Cameron (2000) found that the structure, composition, range use, and stallion behavior of Kaimanawa horses did not meet the predictions of these hypotheses. More recently, Ringhofer et al. (2017) applied hypotheses derived from studies of primate societies to explain multi-stallion groups of horses, but their results showed that horses' male–female relationships differ from those of polygynous primates.

In this study, using a non-invasive methodology, we examined whether body size is a determining factor in differentiating multi-stallion groups from single-stallion groups. Based on what has been found in other species, we hypothesized that larger body size is a favorable trait in stallion competition. Consequently, males in multi-stallion groups may band together to form and defend their own group of females as an alternative strategy to compensate for their smaller size. Additionally, we examined if there were size differences between the sexes and if stallion size predicted the number of females in the group, which we expected to be higher for larger stallions.

2. Methods

2.1. Study area and animals

The study site is in Serra d'Arga, northern Portugal (41°48'22.0"N 8°42'49.0"W), which is a mountainous region, at 824 m above sea level

and is characterized by a temperate Mediterranean climate with Atlantic influence. The landscape features include Atlantic wet and dry heath; low-altitude hay meadows; granite outcrops; and sparse tree coverage. We collected data on Garrano horses, an ancient breed that inhabits the upland heathlands of northwestern Portugal and Spain. In Serra d'Arga, there is a traditional free-ranging husbandry system in place: the horses form social groups, and freely roam and breed year-round. Since 2016, over 200 individuals have been identified at the study site (Inoue et al., 2019, 2020; Mendonça et al., 2020; Ringhofer et al., 2017, 2020). In 2018, we observed 25 groups during the breeding season, four of which were multi-stallion (with two males per group) and two were bachelor groups. Bachelors are stallions who have not yet acquired or managed to maintain females and thus band in all-male groups (Berger, 1986). Although owners do not actively care for the horses, they do sometimes remove individuals, particularly males, and the population is also under predation pressure by the Iberian wolf (*Canis lupus signatus*).

2.2. Body size measurement

As these were feral, untamed horses with little tolerance to human proximity, it would have been impossible to directly approach and manually measure them without resorting to live captures. To avoid this stressful and delicate procedure, we used a non-invasive method to determine body length, which was defined as the total length from the end of the rump to chest, and height, which was from the bottom of the front hoof to withers. We used a Nikon COOLPIX P900 camera to photograph 24 adult males and 26 adult females on three different occasions in June and July 2018. Photos were taken while the subject was in a stand resting position (motionless). All photos were taken with the horses in lateral view and focused on the center of the picture, with no zoom of the lens. Distance between the camera lens and target ranged from a minimum of 6 m to a maximum of 16 m to avoid disturbing the horses while also maintaining a clear view of the target, and was determined with a laser distance meter (Leica DISTO™ s910, Leica Geosystems). A wide range of distances was used because of the varying tolerance levels of different individuals. Then, we photographed a measuring tape that was vertically and horizontally stretched against a board while replicating the distances in the field. In Adobe® Photo-shop® CC 2019, we used the Straighten Tool on the Lens Correction Filter to straighten the measuring tape photos, and we overlapped each photo with its corresponding horse photo. Finally, we extrapolated length and height by aligning the measuring points with the tape and calculated an average body length and height per individual from the three photos taken.

2.3. Statistical analysis

We selected the following variables to test the effects of body length and height (m): sex, group type (single-stallion, multi-stallion, or bachelor), and number of females in the group (ranging from 0 to 8 females, coded as “0”, “1–4” or “> 5”). Analysis was conducted on a total of 50 horses (26♀, 24♂) distributed among 20 social groups, and included 13 single-stallion males, 4 multi-stallion males, and 7 bachelor males. We used a Shapiro–Wilks test to check variables for normality, and ANOVA and T-test to determine if there were significant differences in size between the sexes and in male size depending on group type and number of females. All analyses and graphical outputs were performed with R version 3.5.2 (R Development Core Team, 2016).

2.4. Measurement accuracy and reliability

To test the accuracy of our measurements, we applied the same method to domestic Garrano horses (2♀, 2♂), which were tame and could be handled, and manually measured their length and height three times to calculate an average.

We did obtain some measurements in the field that resulted in a wide range of values between the photos with the highest measure and lowest one of a given horse (from 0 to 23 cm difference), which could potentially affect the strength of our results. Although the exact reason for such values is unknown, it is possible they resulted from human error while replicating distances between the field and tape photos, or accidental miscalculation by the distance meter device. Therefore, we applied the Interquartile Range (IQR) method (Tukey, 1977) to the range of values between the highest and lowest measurements of the three photos per horse, pooled across all the individuals. Data points that scored more than 1.5 IQR below the first quantile or above the third quantile were considered outliers and removed from further analyses. Outlier detection was conducted for the body length and height measurements. Consequently, three single-stallion males and one bachelor male were not considered for body length analysis; and two single-stallion males, one multi-stallion male, and one female were not included for height analysis.

3. Results & discussion

We found no statistically significant differences between manual measurements and the non-invasive approach used for body length ($t(3) = 2.324, p = 0.103$) and height ($t(3) = 1.454, p = 0.242$); therefore, we assumed that the values obtained by the non-invasive methodology for feral horses were reliable. This is a useful tool to remotely measure morphological traits that allows us to avoid disturbing animals and all implications of live captures.

Results showed that size did not significantly differ between males and females (height: $t(42.1) = -1.210, p = 0.233$; body length: $t(43.141) = -0.281, p = 0.780$; Fig. 1). Fig. 2 illustrates the effects of body size on stallion group type and on the number of females in the group, which showed no significant differences (stallion group type, height: $F(2,18) = 1.445, p = 0.262$; body length: $F(2,17) = 1.769, p = 0.201$); number of females in the group, height: $F(2,18) = 2.779, p = 0.089$; body length: $F(2,17) = .329, p = 0.724$). Thus, we assume that other factors may better explain the origins and significance of multi-stallion groups in horse societies.

It is possible that body length and height are not clear indicators of strength, and other traits, such as rank, body condition, or muscle mass, are better suited to gauge fighting ability and male quality. Feh (1990) tested if size differences in stallions were related to reproductive success and found that dominant stallions in multi-male groups were, on average, 18 kg lighter than subordinates, but these differences were not significant. In fact, weight had no correlation with a male's reproductive success or rank, but a stallion's rank influenced its reproductive success. For example, the number of foals sired by young stallions was positively correlated with their rank when they were part of a bachelor group (Bourjade et al., 2009). Moreover, Camargue stallions in multi-stallion groups were shown to be low-ranking, unrelated males of similar age that developed strong bonds during bachelorhood (Feh, 1999). Thus, it is conceivable that the dominance hierarchy and relationships established within bachelor groups may be an indication of the subsequent adoption of alternative mating strategies, such as the formation of multi-stallion groups.

This relationship between males in multi-stallion groups has mostly been described as cooperative. The stallions benefit from their partnership by dominating better quality habitat and increased mare group stability, or because the subordinate stallion trades its help with group defense for the

dominant male's tolerance, and thus gains greater access to females (Feh, 1999; Miller, 1981; Stevens, 1990). However, in a small experiment that temporarily removed the subordinate horses from their groups, Linklater et al. (2013) showed that the dominant stallions successfully defended their mares in the absence of the subordinates. Conversely, stallion–mare aggression significantly decreased, which indicates that female harassment may be a consequence of dominant–subordinate conflict. Stable, long-term stallion–mare relationships are beneficial for the overall reproductive success of mares (Kaseda et al., 1995), perhaps because this helps avoid intra-specific aggression associated with social group changes (Linklater et al., 1999). Therefore, there is strong selection pressure for maintaining long-term male–female and female–female bonds. Multi-stallion groups may simply be the combined result of multiple stallions forming a “consort relationship” with the same mare and male–male dominance behavior during group ontogeny; thus, it may be an artefact of selection for stallion–mare mate loyalty (Linklater et al., 1999).

Typically, we expect males of animal species that form harem-type groups to be larger than females (Pérez-Barbería et al., 2002), because size is an intrinsic factor that influences male competition. However, sexual dimorphism can also be attributed to different ecological needs (Shine, 1989). In many social ungulate species, the sexes are segregated during non-breeding season, which correlates with body size differences between males and females and is likely due to differences in activity budgets (Mysterud, 2000). Neuhaus and Ruckstuhl (2002) hypothesized that male and female plains zebra (*Equus burchelli*) may have evolved the same body size to minimize the costs of behavior synchronization so that they can live in stable mixed-sex groups. Duncan's (1980) results on Camargue horses also seem to support a link between this unusual system that is based on long-term relationships between stallions and mares, and activity budget maintenance. Hence, it is possible that the monomorphism exhibited by horses may be a prerequisite of their social system.

Although there are some morphological structures that can be used to determine sex in some breeds (Kashiwamura et al., 2001; Pinto et al., 2008; Purzyc et al., 2011), horses are considered to have low sexual dimorphism compared with other ungulate species because males and females of the same breed tend to have similar body sizes (Parés-Casa-nova and Allés, 2015). Therefore, we conclude that our findings with Garrano horses are applicable to other feral horses.

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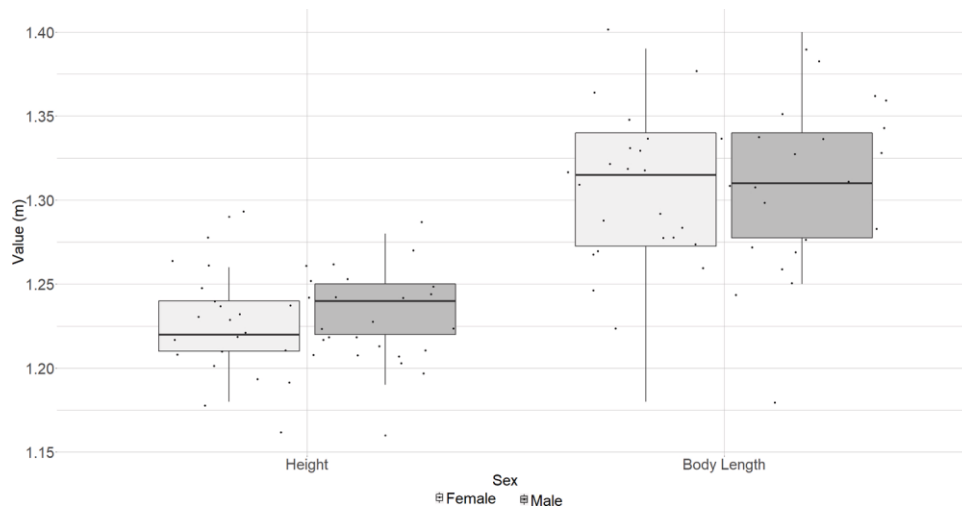


Fig. 1. Average height (m) and body length (m) of mares and stallions.

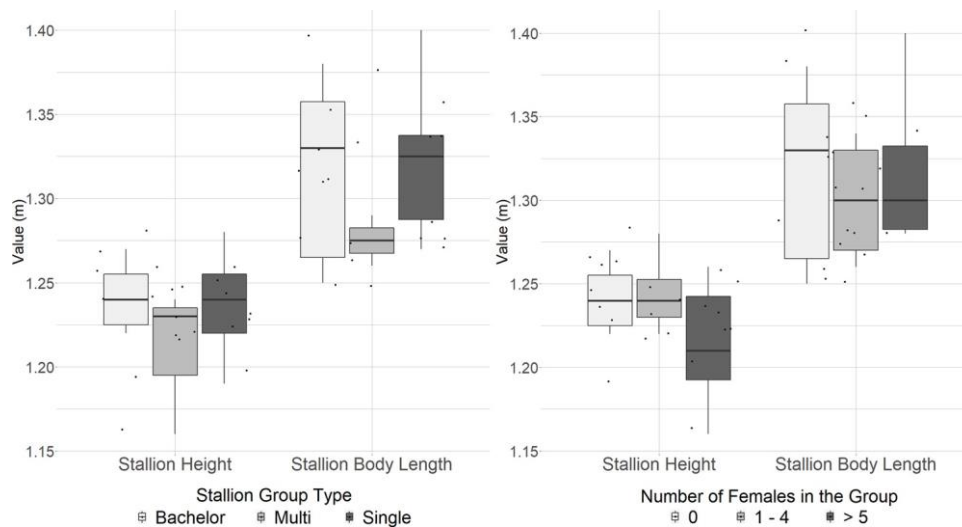


Fig. 2. Average height (m) and body length (m) of stallions based on a) group type: bachelor, single-stallion, or multi-stallion; and b) number of females in the group: 0 females, 1–4 females, or > 5 females.