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NEWS AND PERSPECTIVES

Comparison of the social systems of primates and feral horses: data from a newly established horse research site on Serra D'Arga, northern Portugal

Monamie Ringhofer[1] · Sota Inoue[2] · Renata S. Mendonça[3] · Carlos Pereira[4] · Tetsuro Matsuzawa[3,5,6] · Satoshi Hirata[2] · Shinya Yamamoto[1]

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Abstract Horses are phylogenetically distant from primates, but considerable behavioral links exist between the two. The sociality of horses, characterized by group stability, is similar to that of primates, but different from that of many other ungulates. Although horses and primates are good models for exploring the evolution of societies in human and non-human animals, fewer studies have been conducted on the social system of horses than primates. Here, we investigated the social system of feral horses, particularly the determinant factors of single-male/multi-male group dichotomy, in light of hypotheses derived from studies of primate societies. Socioecological data from 26 groups comprising 208 feral horses on Serra D'Arga, northern Portugal suggest that these primate-based hypotheses cannot adequately explain the social system of horses. In view of the sympatric existence of multi- and single-male groups, and the frequent intergroup transfers and promiscuous mating of females with males of different groups, male–female relationships of horses appear to differ from those of polygynous primates.

Keywords Polygyny · Single-male/multi-male dichotomy · Society · Group-living animals · Sexual conflict

Introduction

On tracing the history of primatology, we came across various studies on feral horses (*Equus caballus*). A pioneer of primate social research, Kinji Imanishi, conducted several studies with his colleagues on feral horse societies on the Toi Peninsula in Miyazaki prefecture (Imanishi 1953) before studying Japanese macaques (*Macaca fuscata*). The individual identification method, a now standard technique for observational research on animals, was first used by Imanishi with feral horses (De Waal 2003; Matsuzawa and McGrew 2008). Using this technique, Imanishi explored the evolution of societies in non-human animals. Although comparative studies of wild primates and horses appear to be rare, recent studies have made comparisons between primates and horses in captivity (Tomonaga et al. 2015; Ringhofer and Yamamoto 2017).

The social system of feral horses is unique among ungulates as they form stable bisexual social groups similar to those of primates (Cameron et al. 2009). The social system of horses is characterized by mixed-sex groups composed of one or a few males with multiple unrelated females and their immature offspring, while some males form bachelor groups (Linklater 2000). Both female and male immatures disperse from their natal groups on

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✉ Monamie Ringhofer
monamie.ringhofer@gmail.com; monamies@hotmail.com

✉ Satoshi Hirata
hirata.satoshi.8z@kyoto-u.ac.jp

✉ Shinya Yamamoto
shinyayamamoto1981@gmail.com

1 Graduate School of Intercultural Studies, Kobe University, Kobe, Japan

2 Wildlife Research Center, Kyoto University, Kyoto, Japan

3 Primate Research Institute, Kyoto University, Inuyama, Japan

4 Université Paris III Sorbonne Nouvelle, Paris, France

5 Institute for Advanced Study, Kyoto University, Kyoto, Japan

6 Japan Monkey Centre, Inuyama, Japan

maturity and thus avoid inbreeding (Monard et al. 1996). Sometimes, adult females change groups because of inter- or intra-sexual aggression in their existing groups (Linklater 2000; Marjamäki et al. 2013).

Why does a society of horses resemble that of some primates but not other ungulates? Comparative studies between societies of primates and horses are important to answer this question and better understand the evolution of animal societies; unfortunately, however, fewer studies have addressed the social system of feral horses than of primates. We investigated the social system of feral horses in light of well-studied primates. We established a new field site to study feral horses in northern Portugal, and collected data on their social organization and social structure, which were compared with existing data to elucidate similarities and differences between the social systems of feral horses and primates.

In this study we focused on the determinant factors of single-male/multi-male group dichotomy in horse groups as compared to primate groups. The social systems of primates differ between species, for example, some species form single-male groups, whereas some form multi-male groups. It should be noted, however, that primates sometimes show flexibility in switching from a single-male to a multi-male group among different populations, even in the same species. Kappeler and van Schaik (2002) proposed the following hypotheses to explain the number of males in a group among group-living primates:

1. The number of females determines the number of males in a group (Mitani et al. 1996). As the spatial dispersion of females influences the grouping pattern of males, the number of males increases as a function of the number of females within that group.
2. The breeding seasonality of females and their degree of reproductive synchrony predict the number of males in a group (Nunn 1999). The temporal synchronization of female mating periods makes it difficult for males to guard and monopolize females, leading to multi-male groups. By contrast, long-lasting and relatively less synchronized female mating periods enable males to monopolize multiple females, plausibly resulting in single-male groups.
3. Predation risk determines the number of males in a group (van Schaik and Hörstermann 1994). As males are more likely to defend their group, more males are present in groups with high predation risk (van Schaik and Hörstermann 1994).

Here, we examined the applicability of these hypotheses to feral horse societies by observing their group composition, group size, ratio of multi- and single-male mixed-sex groups, transfer of adult females, and mating behavior.

Methods

Study site and feral horses

The study site was located on Serra D'Arga, an 825-m-high mountain located in northern Portugal (8°42′N, 41°48′E; Fig. 1). This region has a typical Atlantic climate. The habitat includes pasture, rocky ground, forest, and shrub areas. The study horses, garrano (Fig. 2a) are a pony breed, and one of the oldest breeds originating in Portugal (Morais et al. 2005). The garranos on Serra D'Arga are free-ranging, and some are owned by local people. Although owners do not usually care for or feed the horses, they sometimes cull them, especially young males. The horses are under predation pressure from Iberian wolves (*Canis lupus signatus*) in this region (Álvares 2011; see Supplementary material).

Field observation

We observed horses between 4–22 February and 3–27 June 2016. Because of their long gestation period (11–12 months), breeding and birth seasons occur around the same time (March–August), unlike in some primates. We usually started field observations at ca. 0930 hours and continued until ca. 1800 hours each day. On encountering a group, we recorded its location and identified the group members by their sex, body color, shape of white marks on face and legs, color and side of the mane, and a tag, if any, attached to the ears by the owners. Each group was video-

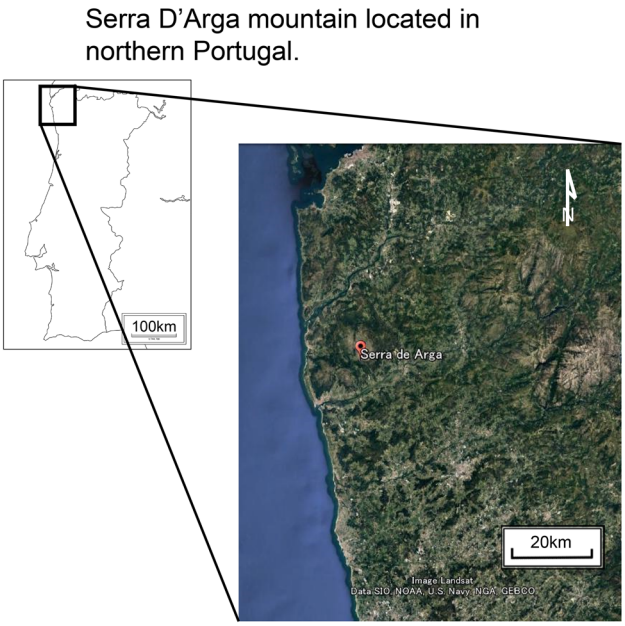

Fig. 1 Location of the study site, Serra D'Arga, in northern Portugal

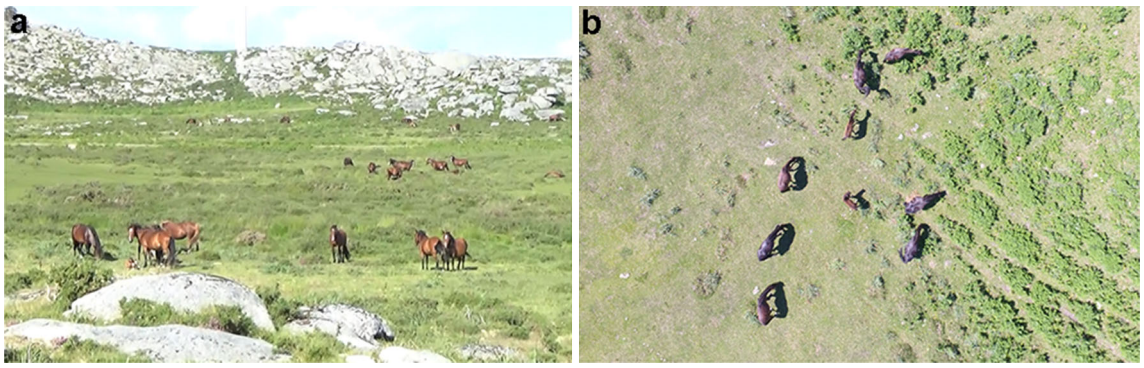

Fig. 2 Feral horses in Serra D'Arga: **a** mixed-sex groups in the field, **b** *aerial view* of a mixed-sex group

recorded from the ground using a camera (Sony HDR-CX535s). In addition, each group was video-recorded from above using a drone (DJI Phantom 3) as an auxiliary device for observing the group members (Fig. 2b). The drone was especially useful in detecting individuals in areas where the ground was uneven. We used one drone at a time to observe each group for approximately 30 min (two flights). In order not to influence the behavior of horses, the drone took off and landed approximately 20 m away from the groups.

Results

Group composition

We identified 208 individuals belonging to 26 groups (adult females, 108; adult males, 45; foals born in 2016, total 45; immature horses born in 2015, total 5; immature horses born before 2014, total 5) (Table 1). Twenty-four of the 26 groups were mixed-sex groups (i.e., contained adults of both sexes), with an average group size (±SD) of 8.2 (±3.3), which was larger than that of most other study sites where group composition data were available (Table 2). One group, Nagano, was a bachelor group in February 2016, but became a mixed-sex group in June 2016; thus, we counted it as a mixed-sex group. The bachelor group size was 6.0 (±3.7) ($n = 3$ in February 2016, $n = 2$ in June).

Of the 24 mixed-sex groups, 18 (75.0%) were single male, and the rest (25.0%) were multi male. The ratio of multi-male groups in this study site was higher than on the Virginia mountain range, USA [4/23 (17.4%) (Gray et al. 2012)] and Cumberland Island, USA [19/171 (11.0%) (Goodloe et al. 2000)], but lower than in Kaimanawa, New Zealand [9/27 (33.3%) (Linklater and Cameron 2000)] and the islands of the Rachel Carson Estuarine Sanctuary, USA [6/12 (50%) (Stevens 1990)]. Predation was observed only on the Virginia mountain range, as in our study site. The average number of females in single-male groups was 5.2 (±2.4), and in multi-male groups it was 2.8 (±1.2); the number of females was significantly higher in single-male than multi-male groups (Wilcoxon rank-sum test, $Z = 2.57$, $P = 0.01$). No such difference was observed in the feral horses of Kaimanawa, New Zealand [average, single male, 1.0–7.4; multi male, 1.0–7.0 (Linklater and Cameron 2000)], the Rachel Carson Estuarine Sanctuary [average, single male, 2.0–2.2; multi male, 1.5–2.3 (Stevens 1990)].

Stability of groups and male–female relationships

We observed several changes in the membership and organization of mixed-sex groups between February and June 2016. Nagano was a bachelor group in February 2016, but converted to a mixed-sex group in June 2016 after one male left and one female joined. We confirmed the transfer of seven adult females (6.6% of all females) to other groups within 3 months. This was assumed to correspond to the annual transfer rate of females reported in other study areas [2.0–29.6% (Mills and McDonnell 2005)].

We observed 14 copulations during all-day observations of Hyogo and Kyoto groups on 13 days. The estrus phase of horses can last for 4–5 days during a 21-day cycle in their breeding season extending from spring to summer (Asa 1986). We recorded two females copulating with males of other groups during their estrus periods; one female of Hyogo group in particular moved between these two groups almost every day and engaged in promiscuous matings.

Discussion

Here, we discuss the social system of feral horses with reference to the previously described three hypotheses regarding the social systems of group-living primates.

Table 1 Social structure of the feral horse groups at the end of the observation periods in February and June 2016

Group type	Group's name	February					June						
		Number of individuals					Number of individuals						
		Male	Female	Immature (male)	Immature (female)	Total	Male	Female	Immature (male)	Immature (female)	Foal	Total (without foal)	Total (with foal)
Mixed-sex	Hyogo	1	5	–	–	6	1	5	–	–	1	6	7
	Kyoto	1	5	–	–	6	1	6	–	–	2	7	9
	Ishikawa	1	3	1[a]	–	5	1	3	1[a]	–	2	5	7
	Nara	1	4	–	–	5	1	4	–	–	0	5	6
	Ibaragi	1	7	1[a]	1[a]	10	1	7	1[a]	1[a]	4	10	14
	Shiga	1	1	–	–	2	1	5	–	–	2	6	8
	Wakayama	1	4	–	–	5	1	5	–	–	2	6	8
	Shizuoka	1	6	1[b]	–	8	1	6	1[b]	–	4	8	12
	Okayama	1	4	1[b]	1[b]	7	1	4	–	1[b]	2	6	8
	Osaka	2	4		–	6	2	3	–	–	1	5	6
	Kanagawa	2	6	1[b]	–	9	2	4	–	–	2	6	8
	Gifu	3	1	–	–	4	–	–	–	–	–	–	–
	Shimane	–	–	–	–	–	1	1	–	–	1	2	3
	Aichi	–	–	–	–	–	1	6	1[a]	1[b]	1	9	10
	Kagawa	–	–	–	–	–	1	4	–	–	3	5	8
	Mie	–	–	–	–	–	1	2	–	–	1	3	4
	Tokyo	–	–	–	–	–	1	12	–	1[b]	4	14	18
	Nagasaki	–	–	–	–	–	1	6	–	–	4	7	10
	Tottori	–	–	–	–	–	1	6	–	–	2	7	9
	Tochigi	–	–	–	–	–	1	6	1[b]	1[a]	2	9	11
	Toyama	–	–	–	–	–	2	2	–	–	1	4	5
	Fukuoka	–	–	–	–	–	2	4	–	–	4	6	10
	Niigata	–	–	–	–	–	2	3	–	–	–	5	5
	Nagano[c]	–	–	–	–	–	4	1	–	–	–	5	5
Sub total	$N = 24$[c]	16	50	5	2	73	31	105	5	5	45	146	191
Bachelor	Hiroshima	2	–	–	–	2	–	–	–	–	–	–	–
	Nagano[c]	5	–	–	–	5	–	–	–	–	–	–	–
	Kumamoto	–	–	–	–	–	11	–	–	–	–	11	11
Sub total	$N = 3$[c]	7				7	11					11	11
Total	$N = 26$[c]	23	50	5	2	80	42	105	5	5	45	157	202[d]

A *dash* indicates that individuals were not found during the specific observation period

[a] Immature horses born in 2015 (estimated)

[b] Immature horses born before 2014 (estimated)

[c] As Nagano changed in terms of group type, it was defined as a bachelor group in February 2016, and as a mixed-sex group in June 2016

[d] Total number of identified individuals in February and June 2016 is 208 (adult females, $n = 108$; adult males, $n = 45$; foals, born in 2016, $n = 45$; immature horses born in 2015, $n = 5$; immature horses born before 2014, $n = 5$)

According to hypothesis 1, the number of females determines the number of males in a group. No evidence in support of this hypothesis was observed in the feral horses. In fact, multi-male groups had fewer females than single-male groups in our study site. No differences have been reported in the number of females in multi-male or single-male groups at other horse study sites (Linklater and Cameron 2000; Stevens 1990). According to hypothesis 2, the breeding seasonality and reproductive synchrony of females predict the number of males. Horses have relatively long breeding seasons, with asynchronous female estrous cycles within a group (Asa 1986).

Table 2 Average group size (including foals) and number of males in mixed-sex groups on Serra D'Arga and at other study sites

	Group size	Number of groups	Existence of predation risk
Serra D'Arga, Portugal (this study)	8.2	23	Yes (wolf)
Tornquist Park, Argentina	8.4	30	Yes (mountain lion)
Alberta, Canada	7.7	23	Yes (wolf and mountain lion)
Assateague Island, USA	9.1	10	No
Toi Cape, Japan	6.0	13	No
Sable Island, Canada	5.5	40–50	No
Pryor Mountains, USA	5.0	44	No
Cumberland Island, USA	4.6	171	No
Grand Canyon, USA	4.5	4	No
Kaimanawa, New Zealand	4.5	36	No

Modified version of Table 4.1. of Mills and McDonnell (2005); we used the published report that mentioned both group sizes and the observed number of mixed-sex groups

According to hypothesis 2, the long-lasting and relatively less synchronized female mating periods enable males to monopolize multiple females. However, single- and multi-male groups exist sympatrically in many feral horse populations, and at some places they even exhibit the same ratios (Stevens 1990). Thus, hypothesis 2 does not apply to feral horse society.

According to hypothesis 3, predation risk determines the number of males in a group. This hypothesis also appears non-applicable to feral horse societies. Comparisons among study sites show that group size in populations with predation risk appears to be larger than in populations without this risk. However, the proportion of multi-male groups is not larger than that of single-male groups, and multi-male groups are not larger than single-male groups, irrespective of the predation risk. Thus, the number of males in a group seems unrelated to predator activity in horses.

These differences between primates and feral horses require consideration of some factors that might be specific to horse society, such as the nature of male–female relationships. Horses show less sexual dimorphism than many polygynous primates (Clutton-Brock and Harvey 1977). The present and previous studies of feral horses have reported multiple female transfers between groups. Moreover, some females mated not only with their group males but also with out-group males in a single estrous cycle. Bowling and Touchberry (1990) reported that, on average, 33% of all foals were not sired by their own groups' males. Given the frequent intergroup transfers and promiscuous mating of females with males of different groups, male–female relationships of horses might reflect a comparatively more equitable society with reduced sexual dimorphism than in many polygynous primates.

It has been suggested that in primate social organization social factors such as infanticide may be more explanatory than environmental factors such as resource distribution or predation (van Schaik and Kappeler 1997). Some authors have proposed that aggression by subordinate males towards females and infants might be a reason for female transfer in feral horse groups (Linklater 2000; Cameron et al. 2003). Feral horse societies might have similar determinant factors to some primate societies, even if the outcome is different. To further explore this possibility, we need more investigations of the social system of feral horses living in various social and ecological environments. We look forward to future comparative studies on primate and non-primate species, leading to new insights into evolutionary mechanisms underlying social systems of group-living animals.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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