

# The interconnection of hierarchy, affiliative behaviours, and social play shapes social dynamics in Maremmana beef cattle

Samuel Bagnato<sup>a,1</sup>, Luca Pedruzzi<sup>a,1</sup>, Jacopo Goracci<sup>b</sup>, Elisabetta Palagi<sup>a,c,\*</sup>

<sup>a</sup> Unit of Ethology, Department of Biology, University of Pisa, 56126 Pisa, Italy

<sup>b</sup> Tenuta di Paganico Soc. Agr. S.p.A., Paganico, 58045 Grosseto, Italy

<sup>c</sup> Natural History Museum, University of Pisa, 56017 Calci, Pisa, Italy

## ARTICLE INFO

### Keywords:

Dominance relationships  
Allogrooming  
Play fighting  
Ethogram  
Beef cattle  
Animal welfare

## ABSTRACT

Dominance hierarchies can be interconnected with behaviours that are essential to manage social living, such as affiliative behaviours and social play, whose importance can already emerge in the early phases of life. Here, we carried out an observational study (*all occurrences sampling*) to investigate the possible interconnection between these three behavioural categories in a group of Maremmana beef cattle ( $n = 44$ , 6–21 months of age) in an extensive breeding system. We found that a clearly linear hierarchy is present in the group, and that the age of the animals positively correlated with their hierarchical ranks. Affiliative behaviours were directed up to the hierarchy: dominants received more affiliative behaviours and subordinates were generally starting the sessions, suggesting that affiliative behaviours may be used by subordinates to bond with dominants for possibly gaining some benefits. Social play mainly consisted of play fighting and dominant subjects played with the highest frequency. However, playful modality was independent from playmates' relative rank position, with longer-lasting sessions being characterized by unbalanced and unreciprocated patterns. This indicates that play fighting in cattle has a competitive rather than cooperative nature and that it may be used as physical training to develop competitive skills in all groupmates. When play fighting was punctuated by affiliative behaviours, the playful sessions lasted longer. In this view, affiliative behaviours can have a communicative value useful in downgrading the competition emerging during play fighting. In conclusion, under naturalistic conditions young animals of beef cattle express all the behavioural repertoire typical of adulthood and their agonistic, affiliative, and playful behaviours are strongly interconnected in shaping social dynamics. Thus, our study suggests that extensive farming conditions are ideal to study the behavioural strategies domestic animals enact to form cohesive social groups. Such information is needed to enhance management and welfare of domestic ungulates.

## 1. Introduction

Many mammal species live in complex societies in which different competitive (e.g., aggression, Preuschoft and van Schaik, 2000) and cooperative domains (e.g., affiliation, social play, Mancini and Palagi, 2009) affect each other concurring in the evolution of social dynamics that can often be predictable starting from immature developmental stages (Silk, 2007). A common strategy to avoid jeopardising group cohesion is the establishment of dominance hierarchies (Preuschoft and Van Schaik, 2000). The position of a subject within the hierarchy depends on intrinsic features such as age, physical attributes and past experience (Sachser et al., 1998; Hubbard et al., 2021). Once dominance

relationships have been defined, overt aggression is not a convenient option and other low-cost behaviours can be enacted (e.g., bodily gestures, Tibbetts et al., 2022). A high dominance rank can also depend on individual extrinsic power, that is the ability to engage in positive behaviours (e.g., social play, Palagi, 2018; social grooming, Schino, 2007) to establish large social networks and gain resources and agonistic support (*Macaca sylvanus*, Berghänel et al., 2011). Therefore, the distribution of power derives from different factors, thus producing a high variability in dominance hierarchies (e.g., despotic vs egalitarian societies, male vs female dominance, stable vs unstable hierarchies, Watts, 2010; Vehrencamp, 1983).

In domestic, feral, and wild ungulates dominance hierarchies are

\* Correspondence to: Department of Biology, University of Pisa, Via A. Volta 4, 56126 Pisa, Italy.

E-mail address: [elisabetta.palagi@unipi.it](mailto:elisabetta.palagi@unipi.it) (E. Palagi).

<sup>1</sup> Samuel Bagnato and Luca Pedruzzi share the first authorship

generally clear (*Hemitragus jemlahicus*, Schino et al., 2022; *Giraffa camelopardalis rothschildii*, Horová et al., 2015; *Lama guanicoe*, Correa et al., 2013; *Bos taurus*, Hubbard et al., 2021; *Sus scrofa*, Puppe et al., 2008) and stable over time (Reinhardt, 1985). Dominance linearity (i.e., the proportion of dominance transitive relationships, for example, if A is dominant over B and B is dominant over C, then A is dominant over C, de Vries, 1995) varies according to resource distribution and monopolisation (*Oreamnos americanus*, Fournier and Festa-Bianchet, 1995), group size (*Equus ferus*, Houpt et al., 1978) and space availability (*Sus scrofa*, Meese and Ewbank, 1973). In ungulates dominance is often related to age, body size, and time spent in the group, whereas they do not seem to be related to sex (Horová et al., 2015; Šárová et al., 2013).

Affiliative behaviours (e.g., allogrooming) can reduce social tension (*Macaca* spp., Judge and de Waal, 1997; *Bos taurus*, Sato et al., 1991; *Sus scrofa*, Norscia et al., 2021), help form coalitions (*Pan troglodytes*, Kaburu and Newton-Fisher, 2015; *Equus ferus*, Mendonça et al., 2021) and establish/maintain bonds between groupmates despite competitive interactions (*Bos taurus*, Val-Laillet et al., 2009; *Capra hircus*, Gorecki et al., 2020; marmosets, Lazaro-Perea et al., 2004). They can also be temporally associated with play fighting (*Equus ferus*, Rho et al., 2007; *Bos taurus*, Reinhardt et al., 1986), possibly conveying positive intents to the partner, thus limiting aggressive escalation (Pellis and Pellis, 1996). Affiliative behaviours can have a polyvalent role depending on whether they are directed down or up to the hierarchy. According to the *Grooming for Commodity Hypothesis* (Šárová et al., 2016) subordinates groom dominants in exchange of other benefits (e.g., tolerance at feeding spots, *Equus ferus*, Feh, 2005; primates, Anzà et al., 2021; Port et al., 2009). The *Grooming for Stability Hypothesis* predicts that, particularly in groups with less strict hierarchies, dominants are central in social dynamics (*Bos taurus*, Šárová et al., 2016) and may provide grooming to subordinates possibly also to limit outranking attempts (primates, Aureli and de Waal, 2000). However, the distribution of affiliative behaviours is not always influenced by dominance ranks, as observed under intensive farming and crowded conditions (*Sus scrofa*, Camerlink and Turner, 2013; Goumon et al., 2020).

Play fighting is common in ungulates' early life stages (Veissier et al., 1998) generally including patterns (or behavioural actions) belonging to different domains (e.g., reproduction or aggression, Palagi and Pellis, 2022). Since play fighting occurs in absence of chronic or intense stress, working on animals reared under extensive condition allows exploring this domain (Palagi and Pellis, 2022). Play allows improve physical skills (*Motor Training Hypothesis*, Byers and Walker, 1995), obtain information on one's own physical abilities (*Self-Assessment Hypothesis*, Thompson, 1998), and increase playmates reciprocal knowledge (*Social Assessment Hypothesis*, Pellis and Iwaniuk, 2000). When including strong competitive elements (Pellis and Pellis, 2017), play can also be strategically used to reassert the dominance status over the playmate (dogs, Bauer and Smuts, 2007). In this perspective, play fighting can range from highly cooperative to strongly competitive, being its modality predictive of its functions (Pellis and Pellis, 2009). Cooperative play helps form social bonds and competitive play helps train for real fights (Mills, 1990).

Here, we tested hypotheses on the possible interconnection between dominance, affiliative, and playful interactions in a group of Maremmana beef cattle (females, heifers, and castrated males, steers), reared in an extensive breeding system, social behaviours strongly neglected in domestic ungulates reared under naturalistic conditions (Sahu et al., 2020). Maremmana cattle is a good model because it has retained genetic and phenotypic similarities with its wild ancestor *B. primigenius primigenius* which further makes the breed interesting per se (Lucifero et al., 1977). Moreover, since Maremmana cows are perfectly adapted to extensive outdoor breeding systems (Lucifero et al., 1977), the data collection of social behaviour under naturalistic conditions is highly feasible.

Since the early stages of life are crucial for the development of social skills in cattle, including dominance relationships (Reinhardt, 1986;

Vitale et al., 1986), we focussed on weaned young beef cattle.

### 1.1. Influence of intrinsic features in shaping the dominance hierarchy

**Hypothesis 1.** Data show that most adult ungulates form linear hierarchies (Schino et al., 2022; Puppe et al., 2008). If dominance relationships are already shaped in juvenile phases, we also expect our group to form a linear hierarchy (*Prediction 1*).

**Hypothesis 2.** If hierarchical ranks depend on physical features (Jensen, 2018; Šárová et al., 2013), we predict ranks to correlate with the animals' age/size (*Prediction 2*). Since no clear sex difference in ranking positions was found in cattle (Blockey, 1979; Stricklin et al., 1980), we do not expect sex to significantly affect animals' ranks (*Prediction 3*).

### 1.2. Influence of extrinsic factors in shaping the dominance hierarchy

**Hypothesis 3.** If affiliative behaviours are used by subordinates in exchange for benefits (e.g., resources, tolerance) with dominants (Šárová et al., 2016), we predict that subordinates not only spend more time providing affiliative behaviours than dominants (*Prediction 4*) but also that they start such sessions more frequently than dominants (*Prediction 5*).

**Hypothesis 4.** If affiliative behaviours are used by dominants to maintain rank relationships stable (Šárová et al., 2016), we predict that dominants not only spend more time providing affiliative behaviours than subordinates (*Prediction 6*) but also that they start such sessions more frequently than subordinates (*Prediction 7*).

**Hypothesis 5.** If play fighting is used as physical and social training for competitive skills (Byers and Walker, 1995), the more unbalanced the play patterns, the longer the play session, independently from playmates' rank difference (*Prediction 8*). Since during play fighting the risk of escalation is real (Palagi et al., 2016), we expect that affiliative behaviours can be used while play fighting to reduce such risk (Pellis and Pellis, 1996) (*Prediction 9*).

**Hypothesis 6.** If play fighting is a tool to assert dominance (Held and Špinka, 2011), we predict asymmetrical social play sessions to be unbalanced against the lower-ranking player (*Prediction 10*).

## 2. Materials and methods

### 2.1. Ethic statement

The present study was purely observational and non-invasive, thus no permit from the Bio-Ethical Committee was needed.

### 2.2. Study site and group

The study was carried out at the *Tenuta di Paganico*, a 1500-hectare organic farm in Paganico (Grosseto, Italy) extensively breeding Maremmana cattle for meat production. The study group was composed of 44 subjects, ranging from 6 to 21 months of life (mean  $\pm$  SD: 8.97  $\pm$  2.21), with 30 heifers (females) and 14 steers (males), all from different mothers and sired by the reproductive male of the adult herd. Weight measures were available for 35 of them (mean weight  $\pm$  SD: 306.3  $\pm$  47.9 Kg), with no difference in weight between the two sexes (*Wilcoxon's rank sum test*,  $W=115$ ,  $p = 0.289$ ). Calves were weaned by mothers and then moved to the fattening group at about 6 months, therefore all the animals knew each other since their birth. All subjects were present in the group since the beginning of the observation period. Although sexual maturity in cattle is often reached before the first year of age

(Gupta et al., 2016), this varies according to the breed (Frateschi and Ducci, 1996). Since in Maremmana breed animals reach full maturity around the third year of age (Jannella et al., 1977; Lucifero et al., 1977), that is much later than in other breeds, our animals were presumably all sexually immature. In our group, males were all castrated in October 2020, well before the beginning of the study. The animals were reared in a fenced hilly area characterised by grassland, shrubs, and woods; moreover, they received supplements of feed at mangers once a day. Close human contacts with animals were highly limited (e.g., monthly physiological sampling for health monitoring).

### 2.3. Data collection and operational definitions

Although data collection took place on different sessions from January to March 2021 (8:30 am-12:30 pm, 2:00 pm-5:30 pm), the first period in January was dedicated to habituate animals to the presence of the observer and to the individual recognition of animals. Videos (Panasonic HC-V180, full HD, 90x; optical zoom allowed recording high-quality frames at long distances; total of 62 h of recordings) were collected at > 25 m from the animals via *subgroup focal sampling* applied to the different subgroups of cattle that naturally split and fused within the same enclosure to have comparable time of observation for each subject as much as possible. Each subgroup was observed for about 1 h, then the focus was shifted on other subgroups. We collected videos of agonistic, affiliative (body contact, rubbing and allo-licking), and social play interactions, coding the initiator and receiver for every pattern (Table S1). An estimation for the time during which each animal was recorded (in the 62 h of recordings) was obtained through the *scan sampling method*. During video analysis, we stopped the video every ten minutes and registered the individuals present in the frame. Then, we summed up all the scans for each subject (e.g., 300 scans in which a subject was observed = 50 h of observation). Individual identification was based on ear tag reading (4-number ID), and physical features (e.g., body size, mantle colour, horns, tail). Since a stressor can have short and mid-term effects on cattle behaviours (Sapolsky, 2000), the distance from the monthly blood sampling was noted down.

Cattle ethograms in literature (Améndola et al., 2016; Bertelsen and Jensen, 2019; Phillips, 2002; Schein and Fohrman, 1955) are often incomplete or not updated, particularly for social behaviours and for the Maremmana breed (Vitale et al., 1986). Thus, we present here a more updated ethogram for social behaviours of Maremmana beef cattle (Table S1, *ethogram*).

#### 2.3.1. Agonistic vs playful behaviours

The distinction of social play from agonistic behaviours is far from being effortless, particularly for play fighting. According to the definition of Burghardt (2005) play includes patterns not completely functional in the context in which they are deployed, they appear exaggerated, incomplete, repeated, or reordered. Play fighting deploys patterns typical of the aggressive sphere that are expressed with a milder intensity (e.g., self-restrained). Moreover, the receiver of the first play fighting pattern does not retreat but actively searches for contact with the playmate to prevent the interaction ending (Held and Špinka, 2011; Pellis and Pellis, 1996). On the contrary, aggressive patterns are not reciprocated by the receiver who normally responds with a submissive posture or fleeing away.

Frame-by-frame video analysis was done via *Pot Player*® (agonistic, affiliative, playful interactions, Table S1). The animals often paused during play bouts for this reason we decided to apply the criterion used by Carter et al. (2019) on another ungulate species to define the temporal window of a session. When two play patterns were separated by more than 60 s, they were considered belonging to different play sessions, and the same criterion was used for affiliative sessions (Carter et al., 2019). For each playful and affiliative session, we coded the identity of the subject initiating or ending the session. Play fighting sessions sometimes included affiliative behaviours and when it

occurred, the time the animals spent exchanging such behaviours was excluded from the calculation of the play session's length. Moreover, for each social play session, we applied the Play Asymmetry Index (PAI) formula, based on advantageous (ADV), disadvantageous (DIS), and neutral (N) play patterns composing the session (Gallo et al., 2022). A pattern was considered as advantageous (ADV) when a player directed a play offensive action or when it was in a favourable position with respect to the playmate. A pattern was recorded as disadvantageous (DIS) when a player assumed a defensive or a self-handicapping position. A neutral pattern (N) is an action that does not provide any ADV or DIS to the player (Gallo et al., 2022). The PAI formula is:

$$\frac{(ADVA + DISB) - (ADVB + DISA)}{(ADVA + DISB) + (ADVB + DISA) + N}$$

Since our subjects never actively performed disadvantageous play patterns, if not just letting the other playmate free to perform an advantageous pattern (e.g., during horn rubbing the receiver lets the actor rub vigorously its horns on the receiver's throat area, see Table S1 for the categorization of each playful pattern), we modified the PAI formula as follows.

$$\frac{ADVA - ADVB}{ADVA + ADVB + N}$$

The index ranges from 0 (perfectly balanced session) to 1 (completely unbalanced session).

#### 2.3.2. Reliability

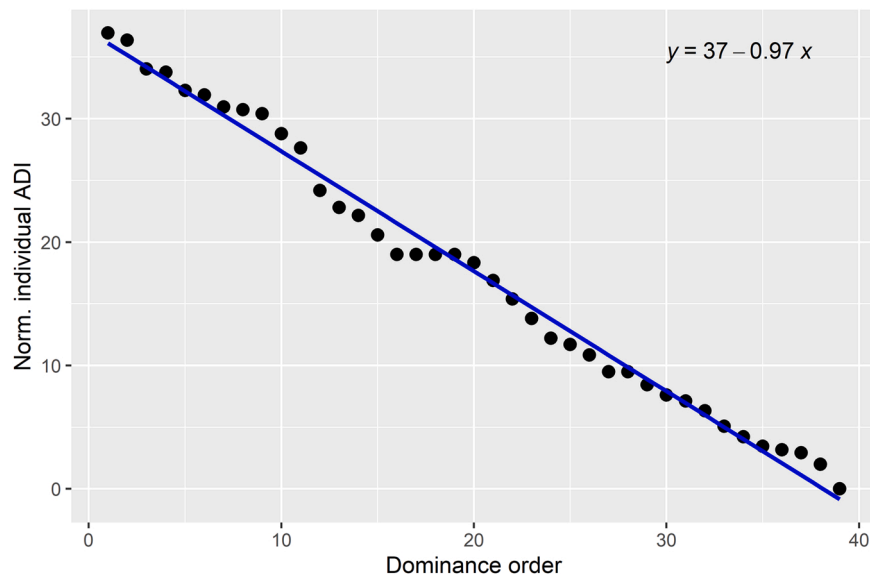
Two coders analysed all the videos in tandem. Before starting the video analyses (62 h of video-recordings), inter-observer reliability was checked between the two coders on about 10% of total videos for individual identification and behavioural context (affiliative, social play, agonistic). The values of *Cohen's kappa coefficient* ( $\kappa$ ) (Cohen, 1960) were higher than 0.9 for both animal identification ( $\kappa = 0.938$ ) and context ( $\kappa = 0.946$ ).

### 2.4. Statistical analysis

Hypothesis 1. We used the normalised Average Dominance Index (normADI, Saccà et al., 2022) to extract the dominance hierarchy and calculate its steepness. The index is an improvement of Normalised David's Scores (David, 1988) and has been introduced to overcome the significant biases in hierarchies' steepness arising when several dyads of the groups do not interact (in our case 439 on 780 possible dyads) (Saccà et al., 2022). We inserted all agonistic behaviours coded (*threats, charges, buttings, pushings, kicks, frontal pushings* as well as *avoidances*, Phillips, 2002; Šárová et al., 2013) in an interaction matrix. All cases with doubtful valence (agonistic/playful patterns,  $n = 12$ ; mounts,  $n = 42$ ) were excluded. We double-tested the hierarchy linearity with i)  $h'$ , the improved version of Landau's  $h$  (Landau, 1951, R package *EloRating* – Neumann and Kulik, 2020) which fills the empty cells with randomised outcomes (de Vries, 1995, with possible biases arising by randomly filling interactions, Saccà et al., 2022) and ii) the Triangle Transitivity,  $t_{tri}$  (Shizuka and McDonald, 2012), an index based on the proportion of transitive triangles among all triangles in a network ( $t_{tri} = 1$  perfect linearity).

Hypothesis 2. We tested the correlation between individual normalised ADIs and Age. Then, we investigated the relationship between rank and sex through a *t-test for independent samples* of males vs. females' ADIs. In addition, since it was not possible to have weight measures for all the 44 subjects, we tested the correlation between Age and Weight (Šárová et al., 2013) for the 35 animals for which 4 wt measures taken at regular intervals during the study period were available (each time all measures taken the same day). This was done to know whether for our beef cattle age can be a reliable indicator of their size.

Hypotheses 3 and 4. We further tested the correlation between individual normalised ADIs and the proportion of time (sec.) spent playing



**Fig. 1.** Graphical representation of the dominance hierarchy of the group of beef cattle ( $n = 39$ ) as the relationship between the dominance order (from 1 to 39) and the normalised Average Dominance Index (Norm. individual ADI) of each subject. The estimated line with its steepness coefficient is indicated.

(*Social play*), receiving (*Aff. behaviours received*) or providing others (*Aff. behaviours given*) with affiliative behaviours on the total time (sec.) of observation calculated for each animal. Then, we analysed the differences of rank scores between the provider and receiver of each affiliative session through a *t-test (one sample)* on normADI differences within the sessions.

To see which factors influenced the response variable *Affiliative session length* (log-transformed) we ran a Gaussian error distribution Linear Mixed Model (LMM, R package: *glmmTMB*). The pair of interacting subjects was included as random factor. The fixed factors considered were the a) difference of ADI between the subjects ( $|normADI\ diff.|$ ); b) sex combination of subjects (*Sex combination*, 0 = same-sex, 1 = different-sex); c) distance from routinary health vet checking (*Sampling*, Ctrl = days distant from sampling, Post1 = hours following sampling, Post2 = day after sampling); d) *Play proximity*, whether the affiliative session was temporally associated with social play (within one minute before and/or after play session; 0 = absence of play within 1 min, 1 = presence of play within 1 min).

Hypothesis 5. We analysed the differences of rank scores between the initiator (inviter) and the other playmate of each social play session through a *t-test (one sample)* on normADI differences within the sessions.

In order to see which factors influenced the response variable *Social play session length* (log-transformed), we ran a LMM (R package: *glmmTMB*). The pair of interacting subjects was inserted as random factor. The fixed factors considered were the a)  $|normADI\ diff.|$ ; b) *Sex combination*; c) *Sampling*; d) *Play Asymmetry Index (|PAI|)*; e) Presence of *Aff. behaviours during play* sessions (Presence = 1, Absence = 0); f) Presence of *Aff. behaviours before play* (1-min-window before a play session; Presence = 1, Absence = 0).

Hypothesis 6. We ran a LMM with PAI as response variable and *normADI diff.* as fixed factor. The interacting subjects were inserted as random factor.

The normality of the variables' distribution was tested through the *Shapiro-Wilk test* (Ghasemi and Zahediasl, 2012) as well as histograms. Homoscedasticity for correlations was verified through the *F test* for variance homogeneity. In cases of non-normality in the distribution of variables and non-homogeneity of their variances we applied non-parametric tests (in the present case the Spearman test). In case of multiple correlations, we applied the *Bonferroni correction* to reduce I-type error (Curtin and Schulz, 1998,  $\alpha_t = \alpha/k$ , with  $\alpha = 0.05$ ;  $k =$  number of correlations). Multicollinearity (Bolker et al., 2009) in

the LMMs was checked with the 'check\_collinearity' function from the R package performance 0.4.4 (by means of VIFs): 'Low correlation' was found for all the fixed factors included in the LMMs (VIF range: 1.01–1.21). The significance of the models was tested comparing the full model with the model including only the random factors (i.e., null model) (Forstmeier and Schielzeth, 2011) through the Likelihood Ratio Test (LRT, Anova with the 'Chisq' argument, Dobson and Barnett, 2018). To estimate each predictor p-value, LRTs were run between the full model and the model not containing that predictor (Barr et al., 2013). To check the models fit and possible overdispersion issues the package DHARMA 0.3.3.0 (Hartig, 2020) was used (for both models, nonparametric dispersion test, dispersion range: 1.0039–1.0059, p-value range: 0.984–0.992). The R-package MuMin 1.43.17 (Bartoń, 2020) was used to calculate the marginal and residual  $R^2$ ; the marginal  $R^2$  indicates the proportion of variance of the response variable explained by the fixed factors only, whereas the residual  $R^2$  indicates that one explained by both fixed and random factors (Nakagawa et al., 2017).

### 3. Results

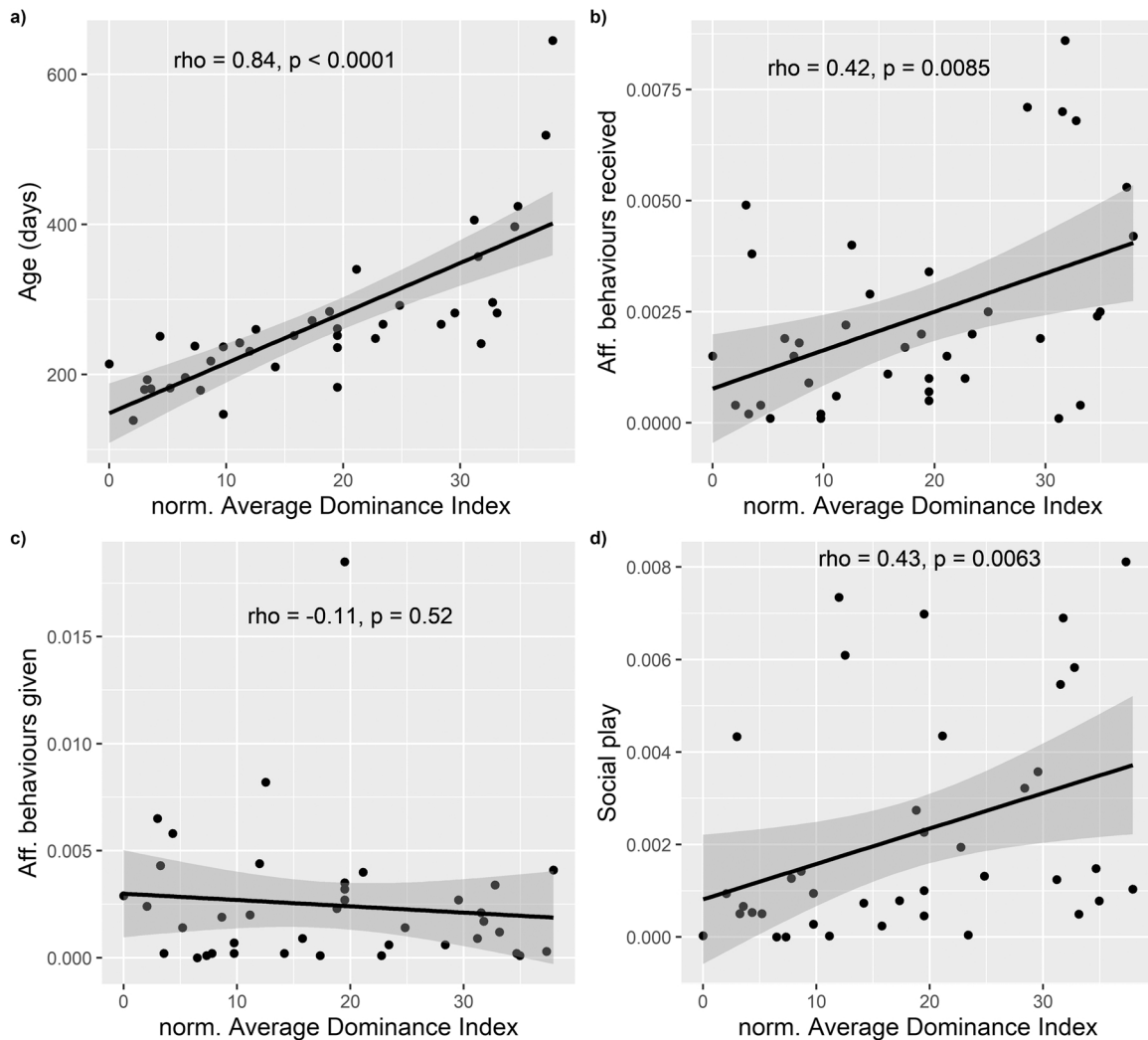
Out of the 44 subjects, 5 were discarded from the analyses since they were recorded for less than 20 h. On the selected group (25 females, heifers, and 14 males, steers, 165–671 days old, average time of observation = 39,17 h), we recorded a total of 599 agonistic interactions, 318 affiliative sessions (mean length=41 s; min=1 s; max=477 s) and 95 social play sessions (mean length=53 s; min=3 s; max=362 s). See Table S1 (*ethogram*) in Supplementary material for behaviours' description.

#### 3.1. Hypothesis 1 - Dominance hierarchy linearity

599 agonistic behaviours in a  $39 \times 39$  square matrix were used to obtain the individuals' rank order, measured with normalised ADIs (Fig. 1). We found a linear hierarchy (Landau's index  $h' = 0.257$ ,  $p$ -value=0.001; transitivity index,  $P_t = 0.990$ ,  $t_{tri} = 0.961$ ,  $p < 0.0001$ ) with a steepness of 0.972. Prediction 1 supported.

#### 3.2. Hypothesis 2 - Intrinsic features shaping dominance hierarchy

We found a positive correlation between normADIs and Age ( $\rho = 0.837$ ,  $p < 0.0001$ , Fig. 2a) and between Age and Weight



**Fig. 2.** Relation between normalised Average Dominance Index and the a) Age of the animals (days), b) Affiliative behaviours received (time spent receiving aff. behaviours/time of observation for the subject), c) Affiliative behaviours given (time spent receiving aff. behaviours/time of observation for the subject), d) Social play (time spent playing/time of observation for the subject). Graphs show Spearman's rank correlation coefficients and p-values. Grey areas represent confidence intervals.

( $r = 0.62$ ,  $p < 0.001$ ), making the age of a subject a reliable indicator of its size. Dominant animals were thus older and larger (*Prediction 2 supported*). NormADIs did not differ according to the Sex of the subjects (*t test*:  $p = 0.41$ ) (*Prediction 3 supported*).

### 3.3. Hypotheses 3 and 4 - Affiliative behaviours and their distribution across the dominance hierarchy

Apart from Age, normADIs positively correlated with the time spent receiving affiliative behaviours ( $\rho = 0.416$ ,  $p = 0.008$ , Fig. 2b). For instance, the top-ranking subject spent almost 3 times more of its time receiving affiliative behaviours compared to lowest ranking one. On the other hand, no correlation was found between individual ranks and the time the subjects spent providing affiliative behaviours ( $\rho = -0.105$ ,  $p = 0.523$ , Fig. 2c) (*Prediction 4 supported*, *Prediction 6 not supported*).

The t-test (one sample) on rank differences in affiliative sessions showed that the initiator was mostly lower-ranking compared to the receiver of affiliative behaviours ( $\text{diff}(\text{normADIs}) = -2.40$ , CI 95%:  $-4.001/-0.800$ ,  $p = 0.003$ ) (*Prediction 5 supported*, *Prediction 7 not supported*).

The full model investigating what affected *Affiliative session length* was significantly different from the null model ( $X^2_6 = 13.100$ ,  $p = 0.023$ , conditional  $R^2 = 0.218$ , marginal  $R^2 = 0.043$ ). The only fixed factor

**Table 1**

Estimated parameters (Estimate), Standard Error (SE), and results of the likelihood ratio tests ( $\chi^2$ ) of the LMM (Gaussian distribution) with *Affiliative session length* (log-transformed, sec.) as response variable. Affiliative sessions = 318. The dyad of interacting subjects was included as random factor. Significant values are in bold.

Affiliative session length. Variance of random factor = 0.311, Std. err. = 4.86					
Fixed factors	Estimate	Std. Error	df	$\chi^2$	p-value
Intercept	3.003	0.184	-	-	-
normADI diff.]	-0.003	0.010	1	0.08	0.778
Sex combination (different)	-0.202	0.167	1	1.460	0.227
Sampling			2	4.520	0.104
Sampling (post1)	-0.444	0.542			
Sampling (post2)	0.290	0.156			
Play proximity (presence)	-0.464	0.157	1	8.740	<b>0.003</b>

affecting the response variable was *Play proximity* (Table 1, Fig. 3). Affiliative sessions were shorter when performed in the minute preceding or following a session of social play (from on average 47 s, with no play session within 1 min, to 30 s, with play sessions within 1 min).

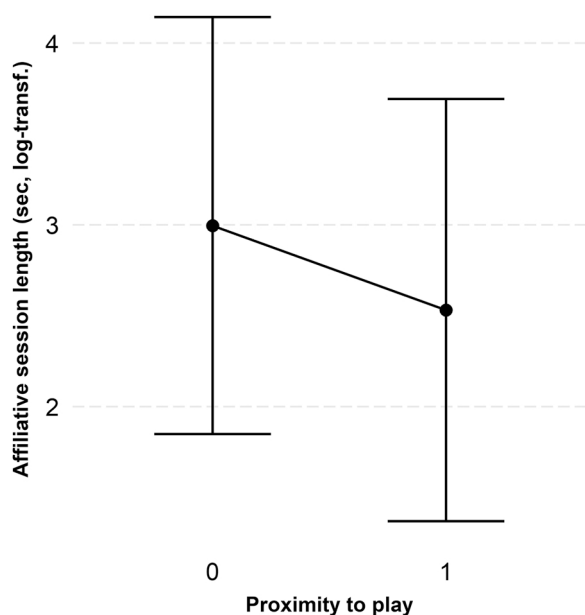


Fig. 3. Plot of the effect of the presence of play within one minute before or after the affiliative session (Play proximity, 0 = absence; 1 = presence) on the length of the affiliative session (Affiliative session length, sec, log-transformed) (Model 1,  $p = 0.003$ ).

Table 2

Estimated parameters (Estimate), Standard Error (SE), and results of the likelihood ratio tests ( $\chi^2$ ) of the LMM (Gaussian distribution) with *Social play session length* (log-transformed, sec.) as response variable. Social play sessions = 95. The dyad of interacting subjects was included as random factor. Significant values are in bold.

Social play session length. Variance of random factor = 0.265, Std. dev. = 0.514					
Fixed factors	Estimate	Std. Error	df	$\chi^2$	p-value
Intercept	2.633	0.252	1	-	-
normADI diff.	0.2087	0.014	1	2.780	0.096
Sex combination (different)	0.013	0.238	1	< 0.0001	0.957
PAI	0.912	0.401	1	4.960	<b>0.026</b>
Sampling (Ctrl)			2	0.400	0.817
Sampling (post1)	0.259	1.047			
Sampling (post2)	-0.123	0.214			
Aff. behaviours during play (presence)	1.669	0.259	1	41.670	< <b>0.0001</b>
Aff. behaviours before play (presence)	-0.074	0.254	1	0.080	0.772

### 3.4. Hypothesis 5 – Play fighting for physical training and affiliative behaviours

NormADIs positively correlated with time spent in social play ( $\rho = 0.430$ ,  $p = 0.006$ , Fig. 2d). For instance, the top-ranking subject spent about 35 times more of its time play fighting compared to the lowest ranking one. The *t*-test (*one sample*) showed that the play fighting sessions were similarly started by higher- and lower-ranking subjects ( $p = 0.48$ ;  $n = 66$  sessions in which it was possible to code who started the session). Since 22% of the play sessions were anticipated by affiliative behaviours (normally performed by the lower-ranking subject of the dyad), we repeated the test on the same subjects excluding the sessions already anticipated by affiliation. Still, no difference in rank was found between the initiator and the other play partner ( $n$  sessions = 47,  $t = -0.145$ ,  $p = 0.886$ ).

The full model investigating what affected *Social play session length* was significantly different from the null model ( $X^2_8 = 44.900$ ,  $p < 0.0001$ ). The significant fixed factors were the |PAI| and *Affiliative*

*behaviours during play* (Table 2). The duration of the session increased when it was punctuated by affiliative behaviours (Fig. 4a) and with its asymmetry (Fig. 4b) (*Prediction 8* and *Prediction 9* supported). Indeed, play sessions punctuated by affiliative behaviours lasted on average almost 4 times more (40 s vs 151 s) than those lacking affiliative behaviours.

### 3.5. Hypothesis 6 – Play fighting to reassert dominance

The null and full model investigating whether the play session was unbalanced in favour of subordinate vs dominant individuals did not significantly differ ( $X^2_1 = 1.611$ ,  $p = 0.204$ ), thus indicating that the relative ranking position of the two players is not predictive of the asymmetry direction of a session (*Prediction 10* not supported).

## 4. Discussion

We found that agonistic, affiliative, and playful interactions are strongly interconnected in our study group of Maremmana beef cattle extensively reared. A linear dominance hierarchy is present (*Hypothesis 1* supported) with the oldest and largest animals occupying the top-ranking positions. Thus, whereas the age (and thus weight) has an effect on ranking, the same does not seem to be true for sex (*Hypothesis 2* supported). Ranking position occupied by heifers and steers does not seem to affect their motivation to provide affiliative behaviours to group members, although dominants received significantly more affiliative behaviours from groupmates scoring lower ranking values (*Hypothesis 3* supported, *Hypothesis 4* not supported). Dominants engaged in higher levels of play fighting, which is rather competitive in this group of beef cattle. The competitive elements of play fighting (i.e., high PAI values) prolong the sessions, making them more effective in training animals for competitive interactions (*Hypothesis 5* supported) rather than for asserting dominance relationships (*Hypothesis 6* not supported). Such playful competition seems to be mitigated by communicative patterns extracted from the affiliative domains exchanged before and during the sessions (*Hypothesis 5* supported). Table 3 summarizes hypotheses, predictions, and outcomes of our study.

A linear dominance hierarchy is present within our group suggesting that dominance dynamics, usually typical in adults, are already present at early stages of life. In linear hierarchies the dominance order is generally based on intrinsic power (Van Schaik and Van Noordwijk, 1988), as found in our study group. Here, the dominance order seems discreetly steep (0.97), meaning that there is significant difference of social dominance between adjacent ranks (Van Schaik and Van Noordwijk, 1988). Even though values of steepness around 1 are often considered typical of despotic groups (e.g., *Pan troglodytes*, Kaburu and Newton-Fisher, 2015; *Macaca* spp., Zannella et al., 2017), we must keep in mind that classic methods used to infer steepness led to underestimations (Saccà et al., 2022), making comparisons rather difficult. Moreover, differences are even more difficult to detect since hierarchy in cattle has been rarely studied under naturalistic conditions (Hubbard et al., 2021). Cattle feed upon widespread and accessible resources (e.g., grass) (Koenig, 2002; Sahu et al., 2020), but competition may still arise leading to the establishment of clear dominance hierarchies in controlled settings (Horová et al., 2015). The positive correlation between rank and age (an indicator of body size) strongly agrees with data from other ungulates (*Ovis canadensis*, Favre et al., 2008; cattle, Blockey, 1979, Stricklin et al., 1980), indicating that experience and physical strength may be strong determinants for ranking status (Šárová et al., 2013; Harcourt and de Waal, 1992). The absence of any relationship between sex and dominance status is consistent with the low size sexual dimorphism in bovines: that trend is maintained also in adulthood independently from the castration of males (Blockey, 1979; Stricklin et al., 1980; Šárová et al., 2013; Hubbard et al., 2021).

Affiliative behaviours were directed up to the hierarchy, with the lowest-ranking animal of the dyad initiating the session more frequently

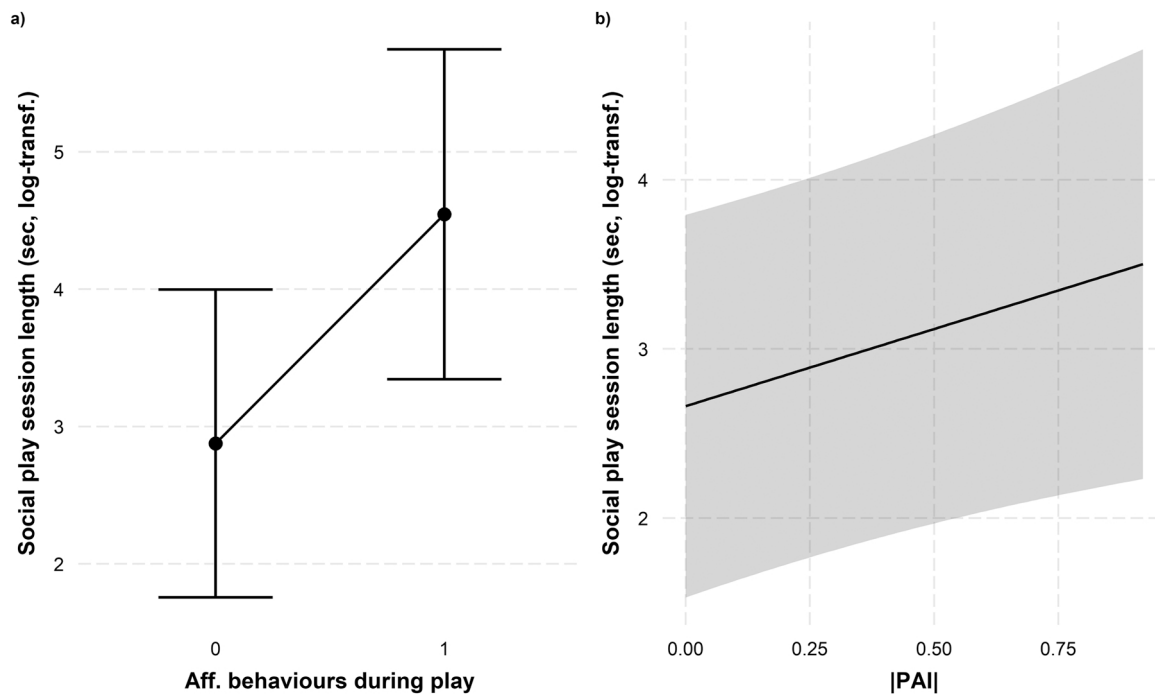


Fig. 4. Plot of the effect of a) the presence of affiliative behaviours exchanged by playmates within a play session (Aff. behaviours during play, 0 = absence; 1 = presence, Model 2,  $p < 0.0001$ ) and b) the asymmetry of the social play session ( $|PAI|$ , Model 2,  $p = 0.026$ ) on the length of the play fighting session (Social play session length, sec, log-transformed). Grey areas represent confidence intervals.

(the subject performing an affiliative bout was on average 2.40 scores lower in ADI than the receiver). Our results are consistent with the *Grooming for commodity hypothesis*, which predicts affiliative behaviours to be used by subordinates to exchange benefits with more dominant animals (Šárová et al., 2016). In ungulates commodities can be protection against predators (Krause and Ruxton, 2002), tolerance during group movements or where resources are clustered (Val-Laillet et al., 2008) such as at resting or feeding mangers (Hamilton, 1971). Our results do not seem to support the *Grooming for stability hypothesis* (Šárová et al., 2016), although we cannot exclude a potential role of grooming in promoting group stability and increasing tolerance of dominants towards subordinates, particularly considering that animals from different ranks provided affiliative behaviours at comparable frequency.

Social play can include cooperative as well as competitive motor actions (Pellis and Pellis, 1996). Similarly to Vitale et al. (1986), we found that social play in Maremmana beef cattle consisted mainly in play fighting, whose sessions lasted longer when the animals played in an unbalanced and unreciprocated way. If play fighting is a tool for assessing one's own physical skills (Bekoff, 2015; Burghardt, 2005; Špinka et al., 2001), it is plausible that the most effective sessions are those strongly asymmetric and that both players are motivated to prolong them. Play is a pleasurable and useful behaviour for all group members with even subordinate animals benefiting from the behaviour (e.g., gaining more social information on playmates and improving physical skills). However, although playful interactions in the group were competitive, they were not influenced by hierarchical ranks of the players. This means that in a play session also dominant subjects can also assume the role of "weaker" thanks to the communicative mechanism called role-reversal (Palagi et al., 2016).

Our findings support the potential competitive nature of social play in this cattle breed and that play might be used in this breed for physical and social training. In our group, this seems supported because the animals occupying higher levels of the hierarchy spent more time playing with other group mates compared to lower-ranking cattle (correlation relationship). Since the most unbalanced sessions are also the longest ones, it is likely that some communicative tactics should be deployed to

limit any risk of escalation (Nolfo et al., 2021). The short affiliative bouts opening and closing the playful sessions could have a similar function. At the same time, those play sessions interspersed by affiliative behaviours lasted on average about four times longer than those lacking any affiliative behaviour. These data together suggest that affiliative contacts may have a role in communicating positive intents during play fighting in Maremmana beef cattle as shown in other species (Pellis and Pellis, 1996, 2017). Signals may be exchanged before the play session, as icebreaker tactic, or be interspersed during an ongoing play session to renew the motivation to play in the companions (Maglieri et al., 2022a). Play signals in mammals are widespread and often rather species-specific (Cordoni et al., 2016; McDonnell and Poulin, 2002; Palagi and Mancini, 2011). Since cows lack a large repertoire of facial expressions and/or vocalisation associated with positively valent events (Laurijs et al., 2021), affiliative behaviours may be useful to downgrade potentially risky situations such as play fighting (Schino, 1998). In juveniles and inexperienced animals, the need for signals to fine-tune play fighting can be even more important. Similar results were found in other ungulates with licking often opening play fighting (cattle, Reinhardt et al., 1986), specifically in more competitive play sessions (horses, Rho et al., 2007). Further investigation may be helpful to clarify the possible meaning conveyed by affiliative behaviours in different contexts. Similar results from other phylogenetically and ecologically distant species (dogs, Cordoni et al., 2016; spotted hyenas, Nolfo et al., 2021) show that long asymmetrical playful sessions are characterized by specific communicative tactics to fine-tune them (dogs, Maglieri et al., 2022b). Importantly, we did not find any relationship between the asymmetry of the session and the relative ranking position of the players, thus underlying the importance of role-reversal tactics in the breed (Palagi et al., 2016). This result makes the use of play fighting by dominants for reasserting their status on subordinates less reliable. The individual motivation to prolong asymmetrical sessions independently from hierarchical ranks suggests that all animals need to gather information to cope with unpredictable and uncertain competitive situations, as predicted by the *Training for the unexpected hypothesis* (Špinka et al., 2001). Play fighting more than any other positive contact trains

**Table 3**  
Summary of hypotheses, predictions, and outcomes of the study.

Hypothesis	Prediction	Outcome	
<b>Dominance hierarchy and intrinsic factors</b>			
<b>Hypothesis 1</b>	Dominance dynamics are already shaped in juveniles	The group of beef cattle forms a linear hierarchy ( <b>Prediction 1</b> )	<b>Supported</b>
<b>Hypothesis 2</b>	Hierarchical ranks are age/size- but not sex-dependent	Dominance ranks correlate with the animals' age/size ( <b>Prediction 2</b> ) No sex effect for the animals' rank position ( <b>Prediction 3</b> )	<b>Supported</b>
<b>Dominance hierarchy and extrinsic factors</b>			
<b>Hypothesis 3</b>	Affiliative behaviours are used by subordinates to bond with dominants ( <i>Grooming for commodity</i> )	Dominants receive more affiliative behaviours ( <b>Prediction 4</b> ) Affiliative behaviours sessions are started by subordinates ( <b>Prediction 5</b> )	<b>Supported</b>
<b>Hypothesis 4</b>	Affiliative behaviours are used by dominants to maintain group stability ( <i>Grooming for stability</i> )	Dominants provide more affiliative behaviours ( <b>Prediction 6</b> ) Affiliative behaviours sessions are started by dominants ( <b>Prediction 7</b> )	<b>Not supported</b>
<b>Hypothesis 5</b>	Play fighting can function as physical training to develop competitive abilities	The more unbalanced the patterns, the longer the play session, independently from playmates' ranks ( <b>Prediction 8</b> ) Playmates communicate their benign intent during play sessions using affiliative behaviours ( <b>Prediction 9</b> )	<b>Supported</b>
<b>Hypothesis 6</b>	Play fighting is used as a tool to assert dominance	Sessions are unbalanced in favour of the higher-ranking player ( <b>Prediction 10</b> )	<b>Not supported</b>

juveniles' physical (e.g., strength, agility) and emotional skills (e.g., fear self-control).

In conclusion, our study shows that under naturalistic conditions beef cattle express all the behavioural repertoire typical of their adult phase (Table S1, *ethogram*). Since our data refers to only one group of cattle breed extensively reared for meat production, they need to be interpreted with caution. Exploring similar topics under the same farming condition, different results can emerge as a function of breeds, group composition (i.e., age) and purpose of farming (e.g., dairy vs beef cattle). However, the analysis of the agonistic, affiliative, and playful categories, that at a first glance appear separated, provides a complex picture of how these three spheres are instead intimately interconnected to shape the social dynamics of this cattle breed. This knowledge is essential to enhance management and welfare of these domestic ungulates. Indeed, all these aspects could not be unveiled under intensive farming conditions, where part of the behavioural repertoire of animals can be inhibited by the limited space availability and crowded conditions, in particular for social play, which is a behaviour performed only without chronic or intense stress.

#### CRedit authorship contribution statement

EP conceived the study; JG provided all the background information useful for data collection and analysis; SB collected the data; SB and LP analysed the videos; SB, LP, EP carried out statistical analyses; SB, LP, EP wrote the manuscript; SB, LP, JG, EP revised the final version of the

manuscript. We thank two anonymous reviewers for their useful comments and suggestions.

#### Conflict of interest

The authors have no competing interests to declare.

#### Acknowledgments

We thank all the staff of the Tenuta di Paganico Soc. Agr. SpA for technical and logistic support in data collection and for their commitment in organic extensive farming and the Department of Agriculture, Food and Environment (DAFE, University of Pisa). We also wish to thank Alice Ripamonti for her help in data collection, and Alessandro Cini and Jacopo Bertocci for their useful critical suggestions.

#### Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.applanim.2023.105868.

#### References

- Améndola, L., Solorio, F.J., Ku-Vera, J.C., Améndola-Massiotti, R.D., Zarza, H., Galindo, F., 2016. Social behaviour of cattle in tropical silvopastoral and monoculture systems. *Animal* 10 (5), 863–867.
- Anzà, S., Demuru, E., Palagi, E., 2021. Sex and grooming as exchange commodities in female bonobos' daily biological market. *Sci. Rep.* 11 (1), 1–10.
- Aureli, F., de Waal, F., 2000. *Natural conflict resolution*, F.B.M. ed., Univ. of California Press, Berkeley.
- Barr, D.J., Levy, R., Scheepers, C., Tily, H.J., 2013. Random effects structure for confirmatory hypothesis testing: Keep it maximal. *J. Mem. Lang.* 68 (3), 255–278.
- Bartoń, K. MuMin: Multi-Model Inference. R package version 1.43.17 (2020). (<https://CRAN.R-project.org/package=MuMin>). Accessed 06 Aug 2021.
- Bauer, E.B., Smuts, B.B., 2007. Cooperation and competition during dyadic play in domestic dogs, *Canis familiaris*. *Anim. Behav.* 73 (3), 489–499.
- Bekoff, M., 2015. Playful fun in dogs. *Curr. Biol.* 25 (1), R4–R7.
- Berghänel, A., Ostner, J., Schülke, O., 2011. Coalitions destabilize dyadic dominance relationships in male Barbary macaques (*Macaca sylvanus*). *Behaviour* 148 (11–13), 1257–1275. <https://doi.org/10.1163/000579511x600628>.
- Bertelsen, M., Jensen, M.B., 2019. Does dairy calves' motivation for social play behaviour build up over time? *Appl. Anim. Behav. Sci.* 214 (2), 18–24.
- Blockey, M.A. d B., 1979. Observations on group mating of bulls at pasture. *Appl. Anim. Ethol.* 5 (1), 15–34.
- Bolker, B.M., Brooks, M.E., Clark, C.J., Geange, S.W., Poulsen, J.R., Stevens, M.H.H., White, J.S., 2009. Generalized linear mixed models: a practical guide for ecology and evolution. *Trends Ecol. Evol.* 24 (3), 127–135.
- Burghardt, G.M., 2005. *The genesis of animal play: Testing the limits*. MIT press. <https://doi.org/10.7551/mitpress/3229.001.0001>.
- Byers, J.A., Walker, C., 1995. Refining the motor training hypothesis for the evolution of play. *Am. Nat.* 146 (1), 25–40.
- Camerlink, I., Turner, S.P., 2013. The pig's nose and its role in dominance relationships and harmful behaviour. *Appl. Anim. Behav. Sci.* 145, 84–91.
- Carter, R.N., Romanow, C.A., Pellis, S.M., Lingle, S., 2019. Play for prey: do deer fawns play to develop species-typical antipredator tactics or to prepare for the unexpected. *Anim. Behav.* 156, 31–40. <https://doi.org/10.1016/j.anbehav.2019.06.032>.
- Cohen, J., 1960. A coefficient of agreement for nominal scales. *Educ. Psychol. Meas.* 20 (1), 37–46.
- Cordoni, G., Nicotra, V., Palagi, E., 2016. Unveiling the "Secret" of Play in Dogs (*Canis lupus familiaris*): asymmetry and signals. *J. Comp. Psychol.* 130 (3), 278–287.
- Correa, L.A., Zapata, B., Samaniego, H., Soto-gamboa, M., 2013. Social structure in a family group of Guanaco (*Lama guanicoe*, Ungulate): Is female hierarchy based on 'prior attributes' or 'social dynamics'? *Behav. Process.* 98, 92–97. <https://doi.org/10.1016/j.beproc.2013.05.003>.
- Curtin, F., Schulz, P., 1998. Multiple correlations and Bonferroni's correction. *Biol. Psychiatry* 44 (8), 775–777.
- David, H.A., 1988. *The method of paired comparisons*, Second ed. Griffin, London (UK).
- Dobson, A.J., Barnett, A.G., 2018. *An introduction to generalized linear models*. Chapman and Hall/CRC.
- Favre, M., Martin, J.G.A., Festa-Bianchet, M., 2008. Determinants and life-history consequences of social dominance in bighorn ewes. *Anim. Behav.* 76 (4), 1373–1380.
- Feh, C., 2005. Relationships and communication in socially natural horse herds. In: Mills, D.S., McDonnell, S. (Eds.), *The Domestic Horse: The Evolution, Development and Management of its Behaviour*, 2005. Cambridge University Press, Cambridge, pp. 83–109.
- Forstmeier, W., Schielzeth, H., 2011. Cryptic multiple hypotheses testing in linear models: overestimated effect sizes and the winner's curse. *Behav. Ecol. Sociobiol.* 65 (1), 47–55. <https://doi.org/10.1007/s00265-010-1038-5>.



- Fournier, F., Festa-Bianchet, M., 1995. Social dominance in adult female mountain goats. *Anim. Behav.* 49 (6), 1449–1459.
- Frateschi, T.L., Ducchi, M., 1996. *Compendio di fisiologia animale. Parte I. Servizio Editoriale Universitario di Pisa.*
- Gallo, A., Zanoli, A., Caselli, M., Norscia, I., Palagi, E., 2022. The face never lies: facial expressions and mimicry modulate playful interactions in wild geladas. *Behav. Ecol. Sociobiol.* 76 (1), 1–13.
- Ghasemi, A., Zahediasl, S., 2012. Normality tests for statistical analysis: a guide for non-statisticians. *Int. J. Endocrinol. Metab.* 10 (2), 486.
- Górecki, M.T., Sochacka, J., Kaźmierczak, S., Gorecki, M.T., Sochacka, J., Kazmierczak, S., 2020. Dominance hierarchy, milking order, and neighbour preference in domestic goats. *Small Rumin. Res* 191. <https://doi.org/10.1016/j.smallrumres.2020.106166>.
- Goumon, S., Illmann, G., Cantor, M., Leszkowová, I., Dostalová, A., 2020. Dyadic affiliative preferences in a stable group of domestic pigs. *Appl. Anim. Behav. Sci.* 230, 105045 <https://doi.org/10.1016/j.applanim.2020.105045>.
- Gupta, S.K., Singh, P., Shinde, K.P., Lone, S.A., Kumar, N., Kumar, A., 2016. Strategies for attaining early puberty in cattle and buffalo: a review. *Agric. Rev.* 37, 2.
- Hamilton, W.D., 1971. Geometry for the selfish herd. *J. Theor. Biol.* 31 (2), 295–311.
- Harcourt, A.H., de Waal, F., 1992. *Coalitions and alliances in humans and other animals.* Oxford University Press, Oxford.
- Hartig, F., 2020. DHARMA: residual diagnostics for hierarchical (multi-level/mixed) regression models. R Package Version 0.3, 3.
- Held, S.D.E., Špinka, M., 2011. Animal play and animal welfare. *Anim. Behav.* 81 (5), 891–899.
- Horová, E., Brandlová, K., Gloneková, M., 2015. The first description of dominance hierarchy in captive giraffe: Not loose and egalitarian, but clear and linear. *PLoS One* 10 (5), e0124570.
- Haupt, K.A., Law, K., Martinisi, V., 1978. Dominance hierarchies in domestic horses. *Appl. Anim. Ethol.* 4 (3), 273–283.
- Hubbard, A.J., Foster, M.J., Daigle, C.L., 2021. Social dominance in beef cattle — A scoping review. *Appl. Anim. Behav. Sci.* 241 (6), 105390.
- Jannella, G.G., Lucifero, M., Secchiari, P., 1977. I parametri riproduttivi della razza bovina Maremmana. *Zoot. Nutr. Anim.* 3, 193–208.
- Jensen, M.B., 2018. The role of social behavior in cattle welfare. *Advances in Cattle Welfare.* Elsevier, pp. 123–155. <https://doi.org/10.1016/B978-0-08-100938-3.00006-1>.
- Judge, P.G., De Waal, F.B.M., 1997. Rhesus monkey behaviour under diverse population densities: coping with long-term crowding. *Anim. Behav.* 54 (3), 643–662.
- Kaburu, S.S.K., Newton-Fisher, N.E., 2015. Egalitarian despots: hierarchy steepness, reciprocity and the grooming-trade model in wild chimpanzees, *Pan troglodytes.* *Anim. Behav.* 99, 61–71.
- Koenig, A., 2002. Competition for resources and its behavioral consequences among female primates. *Int. J. Prima* 23 (4), 759–783.
- Krause, J., Ruxton, G.D., 2002. *Living in groups.* Oxford University Press, Oxford.
- Landau, H.G., 1951. On dominance relations and the structure of animal societies: I. Effect of inherent characteristics. *Bull. Math. Biophys.* 13 (1), 1–19.
- Laurijs, K.A., Briefer, E.F., Reimert, I., Webb, L.E., 2021. Vocalisations in farm animals: a step towards positive welfare assessment. *Appl. Anim. Behav. Sci.* 236, 105264.
- Lazaro-Perea, C., de Fátima Arruda, M., Snowdon, C.T., 2004. Grooming as a reward? Social function of grooming between females in cooperatively breeding marmosets. *Anim. Behav.* 67 (4), 627–636.
- Lucifero, M., Jannella, G., Secchiari, P., 1977. *Razza bovina Maremmana.* Edagricole, Bologna.
- Maglieri, V., Zanoli, A., Mastrandrea, F., Palagi, E., 2022a. Don't stop me now, I'm having such a good time! Czechoslovakian wolfdogs renovate the motivation to play with a bow. *Curr. Zool.* <https://doi.org/10.1093/cz/zoac013> zoac013.
- Maglieri, V., Zanoli, A., Mastrandrea, F., Palagi, E., 2022b. The relaxed open mouth is a true signal in dogs: demonstrating Tinbergen's ritualization process. *Anim. Behav.* 188, 65–74.
- Mancini, G., Palagi, E., 2009. Play and social dynamics in a captive herd of gelada baboons (*Theropithecus gelada*). *Behav. Process.* 82 (3), 286–292.
- McDonnell, S.M., Poulin, A., 2002. Equid play ethogram. *Appl. Anim. Behav. Sci.* 78 (2–4), 263–290. [https://doi.org/10.1016/S0168-1591\(02\)00112-0](https://doi.org/10.1016/S0168-1591(02)00112-0).
- Meese, G.B., Ewbank, R., 1973. The establishment and nature of the dominance hierarchy in the domesticated pig. *Anim. Behav.* 21 (2), 326–334.
- Mendonça, R.S., Pinto, P., Inoue, S., Ringhofer, M., Godinho, R., Hirata, S., 2021. Social determinants of affiliation and cohesion in a population of feral horses. *Appl. Anim. Behav. Sci.* 245 (7), 105496 <https://doi.org/10.1016/j.applanim.2021.105496>.
- Mills, M.G.L., 1990. Kalahari hyenas: comparative behavioral ecology of two species. In: London: Unwin Hyman, Vol. 304. Springer.
- Nakagawa, S., Johnson, P.C.D., Schielzeth, H., 2017. The coefficient of determination R<sup>2</sup> and intra-class correlation coefficient from generalized linear mixed-effects models revisited and expanded. *J. R. Soc. Interface* 14 (134), 20170213.
- Neumann, C., Kulik, L., 2020. Animal dominance hierarchies by Elo Rating. R Package Version 0.46, 11.
- Nolfo, A.P., Casetta, G., Palagi, E., 2021. Play fighting in wild spotted hyaenas: like a bridge over the troubled water of a hierarchical society. *Anim. Behav.* 180, 363–373. <https://doi.org/10.1016/j.anbehav.2021.07.012>.
- Norscia, I., Collarini, E., Cordoni, G., 2021. Anxiety Behavior in Pigs (*Sus scrofa*) decreases through affiliation and may anticipate threat. *Front. Vet. Sci.* 8 (2), 1–14.
- Palagi, E., 2018. Not just for fun! Social play as a springboard for adult social competence in human and non-human primates. *Behav. Ecol. Sociobiol.* 72 (6), 1–14.
- Palagi, E., Mancini, G., 2011. Play and primates: social, communicative, and cognitive aspects of one of the most puzzling behaviour. *Atti Soc. Toscan.-. Sci. Nat., Mem. B* 118, 121–127. <https://doi.org/10.2424/ASTSN.M.2011.32>.
- Palagi, E., Pellis, S., 2022. *Play Behaviour: A Comparative Perspective.* The Routledge International Handbook of Comparative Psychology. Routledge, pp. 202–212.
- Palagi, E., Burghardt, G.M., Smuts, B., Cordoni, G., Dall'Olivo, S., Fouts, H.N., Reháková-Petrů, M., Siviy, S.M., Pellis, S.M., 2016. Rough-and-tumble play as a window on animal communication. *Biol. Rev.* 91 (2), 311–327.
- Pellis, S., Pellis, V., 2009. *The playful brain: venturing to the limits of neuroscience.* Oneworld, Oxford.
- Pellis, S.M., Iwaniuk, A.N., 2000. Adult-adult play in primates: comparative analyses of its origin, distribution and evolution. *Ethology* 106 (12), 1083–1104.
- Pellis, S.M., Pellis, V.C., 1996. On knowing it's only play: The role of play signals in play fighting. *Aggress. Violent Behav.* 1 (3), 249–268.
- Pellis, S.M., Pellis, V.C., 2017. What is play fighting and what is it good for? *Learn. Behav.* 45 (4), 355–366.
- Phillips, C., 2002. *Cattle Behaviour and Welfare.* Cattle Behaviour and Welfare: Second Edition. Blackwell Science Ltd., Oxford.
- Port, M., Clough, D., Kappeler, P.M., 2009. Market effects offset the reciprocation of grooming in free-ranging redfronted lemurs, *Eulemur fulvus rufus.* *Anim. Behav.* 77 (1), 29–36.
- Preuschhoff, S., Van Schaik, C.P., 2000. Dominance, social relationships and conflict management. *Confl. Manag.* 77–105.
- Puppe, B., Langbein, J., Bauer, J., Hoy, S., 2008. A comparative view on social hierarchy formation at different stages of pig production using sociometric measures. *Livest. Sci.* 113 (2–3), 155–162.
- Reinhardt, C., Reinhardt, A., Reinhardt, V., 1986. Social behaviour and reproductive performance in semi-wild Scottish Highland cattle. *Appl. Anim. Behav. Sci.* 15 (2), 125–136.
- Reinhardt, V., 1985. Social behaviour in a confined bison herd. *Behaviour* 92 (3/4), 209–226.
- Rho, J.R., Srygley, R.B., Choe, J.C., 2007. Sex preferences in Jeju pony foals (*Equus caballus*) for mutual grooming and play-fighting behaviors. *Zool. Sci.* 24 (8), 769–773.
- Saccà, T., Gort, G., van de Waal, E., Hemelrijk, C.K., 2022. Reducing the bias due to unknown relationships in measuring the steepness of a dominance hierarchy. *Anim. Behav.* 193, 125–131.
- Sachser, N., Dürschlag, M., Hirzel, D., 1998. Social relationships and the management of stress. *Psychoneuroendocrinology* 23 (8), 891–904.
- Sahu, B.K., Parganiha, A., Pati, A.K., 2020. Behavior and foraging ecology of cattle: a review. *J. Vet. Behav.* 40, 50–74. <https://doi.org/10.1016/j.jveb.2020.08.004>.
- Sapolsky, R.M., Romero, L.M., Munck, A.U., 2000. How do glucocorticoids influence stress responses? Integrating permissive, suppressive, stimulatory, and preparative actions. *Endocr. Rev.* 21 (1), 55–89.
- Šárová, R., Špinka, M., Stěhulová, I., Ceacero, F., Šimečková, M., Kotrbá, R., 2013. Pay respect to the elders: age, more than body mass, determines dominance in female beef cattle. *Anim. Behav.* 86 (6), 1315–1323.
- Šárová, R., Gutmann, A.K., Špinka, M., Stěhulová, I., Winckler, C., 2016. Important role of dominance in allogrooming behaviour in beef cattle. *Appl. Anim. Behav. Sci.* 181, 41–48. <https://doi.org/10.1016/j.applanim.2016.05.017>.
- Sato, S., Sako, S., Maeda, A., 1991. Social licking patterns in cattle (*Bos taurus*): influence of environmental and social factors. *Appl. Anim. Behav. Sci.* 32 (1), 3–12.
- Schein, M.W., Fohrman, M.H., 1955. Social dominance relationships in a herd of dairy cattle. *British J. Anim. Behav.* 3 (2), 45–55.
- Schino, G., 1998. Reconciliation in domestic goats. *Behaviour* 135 (3), 343–356.
- Schino, G., Nazionale, C., 2007. Grooming and agonistic support: a meta-analysis of primate reciprocal altruism. *Behav. Ecol.* 18 (1), 115–120.
- Schino, G., Manzoni, C., Di Giovanni, M., 2022. Social relationships among captive female Himalayan tahr. *Ethology* 128 (10–11), 668–675.
- Shizuka, D., McDonald, D.B., 2012. A social network perspective on measurements of dominance hierarchies. *Anim. Behav.* 83 (4), 925–934.
- Silk, J.B., 2007. The adaptive value of sociality in mammalian groups. *Philos. Trans. R. Soc. B* 362 (1480), 539–559. <https://doi.org/10.1098/rstb.2006.1994>.
- Špinka, M., Newberry, R.C., Bekoff, M., 2001. Mammalian play: training for the unexpected. *Q. Rev. Biol.* 76 (2), 141–168.
- Stricklin, W.R., Graves, H.B., Wilson, L.L., Singh, R.K., 1980. Social organization among young beef cattle in confinement. *Appl. Anim. Ethol.* 6 (3), 211–219.
- Thompson, K.V., 1998. Self assessment in juvenile play. In: Bekoff, Marc, Byers, John A. (Eds.), *Animal play: Evolutionary, comparative, and ecological perspectives.* Cambridge University Press, pp. 183–204.
- Tibbetts, E.A., Pardo-Sanchez, J., Weise, C., 2022. The establishment and maintenance of dominance hierarchies. *Philos. Trans. R. Soc. B* 377 (1845), 20200450.
- Val-Laillet, D., Guesdon, V., von Keyserlingk, M.A.G., de Passillé, A.M., Rushen, J., 2009. Allogrooming in cattle: Relationships between social preferences, feeding displacements and social dominance. *Appl. Anim. Behav. Sci.* 116 (2–4), 141–149. <https://doi.org/10.1016/j.applanim.2008.08.005>.
- Van Schaik, C.P., Van Noordwijk, M.A., 1988. Scramble and contest in feeding competition among female long-tailed macaques (*Macaca fascicularis*). *Behaviour* 105, 77–98. <https://doi.org/10.1163/156853988x00458>.
- Vehrencamp, S.L., 1983. A model for the evolution of despotic versus egalitarian societies. *Anim. Behav.* 31 (3), 667–682.
- Veissier, I., Boissy, A., Nowak, R., Orgeur, P., Poindron, P., 1998. Ontogeny of social awareness in domestic herbivores. *Appl. Anim. Behav. Sci.* 57 (3–4), 233–245.
- Vitale, A.F., Tenucci, M., Papini, M., Lovari, S., 1986. Social behaviour of the calves of semi-wild Maremma cattle, *Bos primigenius taurus.* *Appl. Anim. Behav. Sci.* 16 (3), 217–231. [https://doi.org/10.1016/0168-1591\(86\)90115-2](https://doi.org/10.1016/0168-1591(86)90115-2).

- de Vries, H., 1995. An improved test of linearity in dominance hierarchies containing unknown or tied relationships. *Anim. Behav.* 50 (5), 1375–1389.
- Watts, D.P., 2010. Dominance, power, and politics in nonhuman and human primates. In *Mind the gap*. Springer, pp. 109–138.
- Zannella, A., Stanyon, R., Palagi, E., 2017. Yawning and social styles: different functions in tolerant and despotic macaques (*Macaca tonkeana* and *Macaca fuscata*). *J. Comp. Psychol.* 131 (3), 179.