Personality homophily drives female friendships in a feral ungulate

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Abstract

Friendships, exhibited by both humans and non-human animals, have considerable adaptive benefits. In humans, similarity or homophily in personality is considered a proximate mechanism driving friendships, yet little is known about the behavioural 'decision rules' underlying animal friendships. Some empirical research suggests that animal friendships can be driven by personality homophily. However, these studies are restricted to non-human primates, limiting our understanding of the mechanisms of friendships. We investigated a feral population of water buffalo (*Bubalus bubalis*) to determine whether homophily in personality drives friendships in this 'non-model' social species in free-ranging environmental conditions. We conducted observations on females (*n=30*), and assessed their friendships and personalities. Close spatial proximity served as a behavioural indicator of friendship, validated by affiliative body contact. An objective 'bottom-up' method revealed three personality traits – *social tension*, *vigilance*, and *general dominance*. We found that females with comparatively lower personality differences in social tension and general dominance traits exhibited significantly higher close spatial associations. Our findings show that friendships in buffalo can form based on personality homophily, a decision rule attributed predominantly to primates. We discuss these findings in light of buffalo socioecology but emphasise their implications in the broader evolutionary context of animal personalities and friendships.

Keywords

Buffalo, Feral ungulates, Inter-individual differences, Partner choice, Social bonds, Social relationships

Introduction

In social species, including humans, the strength of affiliative 'ties' in a social network is not homogenous, indicating varying degrees of relationships among individuals. Preferential strong social associations or friendships are of particular interest as they positively correlate with health, well-being, and survival benefits [1,2]. Although conceptualised relatively recently in non-human animals (hereafter, animals) [3], growing convergent evidence suggests that human-like friendships can form in animals [4,5]. Similar to humans, animal friendships can be stable, long-lasting [6,7], and form beyond the extent of kin relationships [8]. The primary evolutionary explanation of friendship lies in their low levels of uncertainty, where, in comparison to a non-friend, a friend provides assured fitness benefits, and these benefits surpass the costs of maintaining friendships [9]. For instance, friendships foster cooperation, which minimises the probability of 'cheating' [10–13]; the strong emotional underpinning of friendship can act as a 'social buffer' during aversive situations, improving the physiological states of the friends and enhancing their survival [14–16]; and friendships, even same-sex, can positively influence reproductive outputs [17,18]. Although the evolutionary implications are well established, the proximate mechanisms of animal friendships are relatively understudied. Consequently, empirical evidence on the behavioural decision rules that apply in a 'biological market' to choose preferred partners or friends is lacking [19].

Several behavioural decision rules have been proposed as proximate mechanisms of animal friendships [20], of which the 'homophily principle' received much attention. The homophily principle, proposed originally to characterise human social networks, suggests that individuals similar in terms of their age, gender, ethnicity, and interests are more likely to become friends [21]. To some extent, these propositions fundamentally overlapped with that of another behavioural decision rule, the symmetry-based reciprocity [22,23]. Yet, friendships in animals can form irrespective of age and sex, and thus, demographic variables could not solely explain the emergence of friendships [24]. Personality – the consistent inter-individual differences [25] – due to their immense adaptive values [26], have been proposed as an alternate mechanism influencing friendships. Similarities or differences in traits are calculated at the dyadic levels to evaluate how personalities may influence friendships. Interestingly, when extended to personalities, researchers have found strong evidence of homophily explaining the emergence and sustenance of friendships in both humans [27,28] and animals (chimpanzee [29], bonobo [30], Assamese macaque [31], baboon [32]). Yet, given that these findings are restricted to (non-human-)primates, testing the hypothesis in phylogenetically diverse taxa is required to ascertain if personality homophily is a general behavioural decision rule of friendship.

Ungulates represent a wide range of species with varying social organisations [33], providing a suitable system to expand the investigation of the emergence of friendships. Several ungulate species exhibit complex sociality patterns, including marked preferences for specific group members over others (e.g., cattle [34], goat [35], Przewalski's horse [36], bison [37], water buffalo [38]). However, existing research has predominantly used demographic characteristics, e.g., age and sex, often coupled with kinship and dominance rank relationships, to explain sociality patterns in 'non-random' or heterogeneous networks. In recent years, studies have assessed the personality traits of various ungulate species and identified their influence on cognitive performance and decision-making [39,40], autonomic nervous system reactivity [41], dominance hierarchy [42], and welfare [43], among others. Yet, to our knowledge, no systematic attempt has been made to investigate the effects of personality homophily on the emergence of ungulate heterogeneous social networks, including friendships. Moreover, most research on ungulate social behaviour and personality is performed in captivity, often as livestock, thus partly limiting the broader ecological value of the findings [44].

Here, we studied a feral and free-ranging population of a highly social ungulate species, the water buffalo (*Bubalus bubalis*). To assess friendships in female buffalo, we utilised two behavioural indicators, proximity and affiliative body contact [20]. Unlike non-human primates and many ungulate species, allogrooming, a strong indicator of social bonds, is predominantly absent in buffalo [45]. However, in species with limited direct affiliative interactions (e.g., allogrooming), social associations (e.g., proximity and body contact) can sufficiently capture the varying social bonds among individuals [46]. We further conducted extensive behavioural observations and objectively assessed the consistent inter-individual differences or personalities in female buffalo. Notably, we used a 'bottom-up' approach to assess personalities; hence, traits were not predetermined [47–50]. We hypothesised that if friendships among female buffalo are formed based on personality homophily, then homophily in personality is a general behavioural decision rule for partner preference. In particular, we predicted that lower score differences in social personality traits would be positively associated with higher dyadic proximity values.

Methods

A. Study area and population

We conducted this study on a feral and free-ranging population of water buffalo present in Pui O in the Southern Lantau Island of Hong Kong SAR, China. Pui O is a small village at the edge of Lantau South Country Park, and the marshlands of Lo Wai Tsuen (22°14'32.7" N

113°58'42.3" E) and Lo Uk Tsuen (22°14'29.3" N 113°58'31.1" E) in Pui O are home to two different herds of feral buffalo. At the beginning of the study, the Lo Wai Tsuen herd had a size of 19 (females = 7, males = 12), whereas the Lo Uk Tsuen herd was comprised of 29 individuals (females = 25, males = 4), of which two females were below two years of age (i.e., calves). We collected data on thirty adult females (age range: 4 to 19; mean age in years ± standard deviation = 10.38 ± 4.33) from the two different herds (Lo Wai Tsuen = 7, Lo Uk Tsuen = 23, **Table S1**, Supplementary Information) between 17th July 2023 and 6th February 2024, including a wet and a dry season [51]. While the number of females remained the same throughout the study period, the number of males changed in both herds due to death and dispersal. Two male buffalo from the Lo Wai Tsuen herd dispersed in October, and one individual died in late December (due to natural causes). One male buffalo from the Lo Uk Tsuen herd dispersed in January. Although the two herds live adjacently, inter-herd interactions among females were never observed (personal observations, D.B., 2023-2024, also see [52]). The buffalo fed on grass and other natural vegetation but occasionally (three to four times a week between December and February) received supplementary food (hay and sweet potato leaves) from local citizen groups. Fresh water was available *ad libitum* from small waterbodies in and around the marshlands.

A cattle management team from the Agriculture, Fisheries and Conservation Department of Hong Kong (AFCD) routinely sterilised and managed the buffalo population [53]. All adult females were sterilised except one from the Lo Uk Tsuen herd, and their status did not change during the study period. While over 50% of the adult females (16 out of 30) had numbered ear tags (administered by the AFCD), we relied on morphological features, such as horn shape and structure, relative horn length and distinct scar marks, to identify the remaining individuals. Subsequently, a photo catalogue was prepared to ensure the reliable identification of the individuals. The individual age details were collected from a local non-government citizen group, documenting the buffalo population's demographic information over the past 20 years. However, data on kin relationships among the individuals were not comprehensive and, therefore, not used.

B. Ethical declarations

Ethical approval was obtained from the Animal Research Ethics Sub-Committee of City University of Hong Kong. The behavioural observations of buffalo were conducted from a distance of at least 20 m without direct human intervention. We adhered to the ethical guidelines of the ASAB/ABS for conducting the research [54].

C. Data collection

Continuous focal and scan sampling methods were used to collect behavioural data [55]. Each observation day was divided into three time periods: morning (0900-1159 hours), afternoon (1200-1459 hours), and late afternoon (1500-1800 hours), and each period was equally sampled. An extensive ethogram was developed with all behaviours exhibited by the buffalo (**Table S2**, supplementary information), which was used during data collection and coding.

Focal sampling

Each continuous focal observation session was 20 minutes long. We collected 720.03 ± 0.32 minutes (mean ± standard deviation) of focal data per individual. Thus, each individual was observed a total of 36 times. We used a semi-randomised order to observe the individuals in different time periods on an observation day, and the same individual was not observed more than once per day. We conducted one to nine focal observations daily (5.17 ± 1.96 focal observations/day), at least three times a week. Focal data were recorded using a video camera (Panasonic HC-V785) mounted on a tripod or collected live using digital data sheets. All state (durations) and point (frequencies) behaviours of the focal individuals, as well as their interactions with non-focal herd members, were noted using the ethogram.

Herd scan sampling

We followed predetermined routes during scan sampling. The sampling distances of Lo Wai Tsuen and Lo Uk Tsuen were 2.1 km and 2.3 km, respectively. The same routes had to be walked more than once to cover the sampling area, but data were recorded only for the first time. During each scan, we recorded the spatial positions of the individuals relative to each other in a herd. We collected data on the frequency of two levels of dyadic spatial positions: dyadic proximity (one body length distance to each other) and affiliative body contact (body parts of two individuals excluding legs or horns touching while standing, sitting, or lying down) (see **Figure S1** and **Table S2**, supplementary information). We conducted 3 – 5 scans per day (3.84 ± 0.74 scans/day) at least twice a week. The interscan interval was 30 minutes, and we conducted 300 scans of each herd. Notably, all individuals from their respective herds were present during all the scans.

D. Data analyses and statistics

Coding

Videos were played using Pot Player (version 240315, 1.7.22129) and coded in a frame-by-frame manner. Following the ethogram, we coded the duration (in seconds) and frequency of all relevant state and event behaviours, respectively (cf. **Table S2**). Since each individual

was observed for the exact duration (i.e., 720 minutes), no time correction was deemed necessary. D.B. coded all the videos and compiled them with the focal data recorded in digital datasheets. Another person, unaware of the goals of the study, coded 5% and 10% of the focal and scan data, respectively. The reliability between D.B. and the blind coder was excellent (Intraclass correlation tests: focal data - ICC (3,k) = 0.93, $p < 0.001$; scan data - ICC (3,k) = 0.95, $p < 0.001$).

Assessment of friendships

We created all possible combinations of dyads at the herd level (Lo Wai Tsuen herd = 21 dyads and Lo Uk Tsuen herd = 253 dyads). From the herd scans, the frequencies of proximity and affiliative body contact were used to calculate a dynamic dyadic sociality index (DSI) [56,57], a widely accepted and validated indicator of friendship in animals. Dyadic proximity and body contact frequencies were divided by the respective population mean values to calculate corresponding index (i.e., dyadic proximity index and body contact index) values. These scaled index values were combined and averaged to obtain the DSI values. However, the data on the frequency of body contact was zero-inflated, with only close to 30% of the potential dyads exhibiting affiliative body contact. To avoid any statistical model convergence issues, we chose dyadic proximity index as the only indicator of friendship (see [20,58]). Nevertheless, we investigated the validity of dyadic proximity index by comparing it with the body contact index (Spearman rank correlation: n=274, $\rho = 0.42$, $p < 0.001$). This moderately strong positive correlation indicates that the dyadic proximity index sufficiently captured affiliative social relationships or friendships. On average, the proximity index had a value of one (range = 0.15 to 2.19), with higher values indicating stronger friendships. For instance, a dyadic value of 2.19 indicates 2.19 times stronger friendships between two individuals than the average.

Assessment of personality

A standardised 'bottom-up' approach was used to assess the personality traits [47–49], where any potential bias of predetermined clustering of variables could be avoided. By definition, personality traits should be consistent across time and contexts [25]; therefore, we divided the focal data into two phases (with 360 min/focal individual for each phase) to investigate whether they were repeatable. The repeatability of behavioural variables was assessed using a two-way mixed model intraclass correlation (ICC (3,1)) test [47–49]. Forty-eight behavioural variables (cf. **Table S2**) were considered for the bottom-up approach. However, variables with low frequencies were dropped before conducting the ICC analysis. Twenty-seven variables were dropped as more than half of the individuals did not exhibit them, i.e., the variables had zero occurrences. Subsequently, twenty-one variables were retained for

the ICC analysis (**Table S3,** supplementary information). We used a conservative ICC cut-off value of 0.5 for a variable to be considered repeatable [59]. Fourteen of the twenty-one variables were repeatable, with ICC values ranging from 0.521 to 0.850 (**Table S3**).

A principal component analysis (PCA) was conducted using the fourteen repeatable variables. The average values of the repeatable variables between the two phases were calculated, standardised, and included in the PCA. However, due to low Kaiser-Meyer-Olkin sampling adequacy (MSA) values (MSA cut-off value = 0.6) and inadequate percentage communality values (communality cut-off value = 70%) [60], the number of variables was further reduced to six by a step-by-step process (cf. [47,48]). The percentage of communalities of the remaining six variables ranged between 73.02 to 91.33, with an overall MSA value of 0.69. A scree plot was generated using an unrotated PCA, and the eigenvalue of each potential principal component (PC) was retrieved. The number of PCs was subsequently decided based on the eigenvalues (with eigenvalue ≥1) and by visual inspection of the scree plot (**Figure S2**, supplementary information) [60]. All other assumptions of PCA were met (Bartlett test: $p < 0.001$, and cumulative variance explained by PCs > 60%). As personality traits can be correlated and form behavioural syndromes [61], we used an oblique rotation technique (direct oblimin rotation). The factor loadings ≥ 0.6 (positive and negative) were considered significant [62].

We extracted three PCs (or personality traits), cumulatively explaining 81.15% of the variance. The three PCs extracted from the PCA were labelled based on the behavioural variables that loaded on them (see **Table 1**). PC1 had three positively loaded variables: approach, self-groom, and avoid. We labelled it as *social tension*. PC2 included only one variable, vigilance; hence, it was given the same label, i.e., *vigilance*. PC3 had two loaded variables, sit and displace, loaded positively and negatively, respectively. We labelled PC3 *general dominance*. From each PC or personality trait, individual factor scores (synonymously personality scores) were extracted, and score differences were calculated for all combinations of dyads. As personality traits are often considered age-independent behavioural constructs, we tested for correlations between individual age and personality scores for the three traits separately. Personality traits and age had no significant relationships (Spearman rank correlation tests, social tension: $\rho = -0.01$, $p = 0.93$, vigilance: $\rho = -0.01$, $p = 0.92$, general dominance: $\rho = 0.006$, $p = 0.97$).

Table 1. The rotated principal components or buffalo personality traits with variable loadings and their percentages of variance, and percentages of attribute communalities of the behavioural variables.

Variables	Social tension	Vigilance	General dominance	% Communalities
Approach	0.87			73.12
Self-groom	0.86			77.27
Avoid	0.76			73.02
Vigilance		0.97		91.33
Sit			0.80	85.98
Displace			-0.64	83.62
% Variance	41.30	20.10	19.75	

Variable loadings of >±0.6 are considered significant.

Effects of personality trait- and age- difference on friendships

A generalised linear mixed-effect model (GLMM) analysis was conducted to investigate the effects of personality score- and age- differences on dyadic proximity index values. We used a Gaussian error distribution with an 'identity' link function. In the full model, the dyadic score differences of each personality trait and absolute dyadic age differences were included as fixed effects and the proximity index as a response variable. Individual identities of a dyad (i.e., individual 1 and individual 2) were included as random effects. The null model included the response variable and the random effects but lacked fixed effects.

Assessment of dominance hierarchies and their effects on friendships

Some behavioural variables (i.e., avoid and displacements), which constituted the social tension and general dominance personality traits, are often used in combination with other behaviours, such as agonistic interactions, to construct dominance hierarchies [63]. However, we found that these direct interactions were very rare during scans, leading > 94% 'unknown' dominance rank relationships among the individuals. Thus, dominance hierarchies could not be constructed based on the data collected during scans. Yet, to investigate whether dominance hierarchies were associated with friendships, we assessed hierarchies based on our overall continuous focal data. We created four frequency-based matrices per herd where all individuals were placed as initiators and receivers of avoid, displace, physical aggression, and flee behaviours (see **Table S2** for definitions). Subsequently, we built combined matrices, each for a herd, that followed consistent directional patterns of the behaviours (i.e., avoid, being displaced, being physically

aggressed, and flee). We used a Bayesian Elo-rating method to assess herd-level hierarchies [64]. The method involved the calculation of winning probabilities from the combined matrices. Both the herds had low to moderately steep dominance hierarchies (Steepness: Lo Wai Tsuen = 0.61 ± 0.07, Lo Uk Tsuen = 0.53 ± 0.04). Upon construction, individuals were plotted ordinally along their respective hierarchies based on the estimated Elo values. The ordinal rank differences were calculated for the dyads and standardised to account for the varying herd sizes. Since personality and dominance data are not independent, to avoid any bias of data dependence, rank difference was not included as a fixed effect in the GLMM that investigated the effects of age and personality differences on friendships. In a separate GLMM with a Gaussian error distribution and 'identity' link function, dyadic rank difference was included as a fixed effect and the proximity index as a response variable. Individual identities of a dyad were included as random effects. The null model included the response variable and the random effects but lacked the fixed effect.

Statistical packages

All statistical analyses were performed in R (version 4.3.1) [65]. ICC analyses were conducted using the *psych* package [66]. We used *Elosteepness* package to construct the dominance hierarchies [64]. We used the package *glmmTMB* for the GLMM analyses [67]. The null vs full model comparisons were checked with the *lmtest* package [68]. Collinearity among fixed effects was investigated using the *performance* package [69], and a variation inflation factor (VIF) of >3 was considered a threshold for high correlation [70]. GLMM model diagnostics (normality assumptions) were checked using the package *DHARMa* [71]. The significance value was set at 0.05 for all statistical tests.

Results

We found significant relationships between personality trait differences and the dyadic proximity index (**Table S4,** supplementary information). Lower dyadic score differences in social tension were associated with higher dyadic proximity index values (GLMM: z = -5.134, Cohen's d = 0.62, 95% CI = [0.38, 0.86], p <0.001, **Figure 1a**). Differences in vigilance did not affect the dyadic proximity index (GLMM: z = 0.672, p = 0.50, **Figure 1b**). Like social tension, dyads with lower score differences in general dominance had higher proximity index values (GLMM: z = -4.440, Cohen's d = 0.54, 95% CI = [0.30, 0.77], p <0.001, **Figure 1c**). We found no significant effect of age differences on the dyadic proximity index (GLMM: z = 1.483, p = 0.13). These results indicate that dyads with more similar social tension and general dominance but not age differences were more likely to be in close proximity than dyads with greater trait differences. This full model differed from the null model (Likelihood

ratio test: χ^2 = 56.689, p <0.001). We found no collinearity among the fixed effects (VIF range: 1.01 - 1.12), and the model residuals followed normality assumptions. We did not find any effect of dominance rank differences on dyadic proximity index values (GLMM: z = -0.166, p = 0.87, **Table S5,** supplementary information).

Discussion

The emergence of friendships in animals has long been considered a phenomenon governed by similarities in demographic characteristics, such as age and sex [4]. However, the sustenance of age- and sex-independent friendships has impelled researchers to propose alternate explanatory mechanisms, like homophily in personality [29]. Yet, empirical research explicitly testing homophily as a behavioural decision rule of friendship is mainly restricted to primates. We investigated adult same-sex friendships in a free-ranging and feral population of a social ungulate species, the water buffalo [72]. Our results show that non-random female-female social associations can form in feral buffalo, where stronger associations indicate friendships [20], and homophily in certain personality traits can significantly predict friendships. Similarities in age and dominance rank relationships did not explain the dyadic social associations and friendships. We highlight that homophily in personality is a proximate behavioural decision rule of friendship that applies to species beyond primates.

Friendships in buffalo

The dyadic proximity index, validated by affiliative body contact, captured the differential strengths of buffalo social associations, including friendships. Friendships in buffalo can have considerable socio-ecological and adaptive implications, which can range from foraging and collective movement to resting. The ‘conspecific attraction hypothesis’ suggests that the presence of conspecifics can be used as social cues during foraging site selection, especially when resources are patchily distributed [73] (also see [74]). However, social aggregations during foraging are often considered a by-product of sharing space (i.e., random associations) and not outcomes of preferential associations. Although empirical testing of such assumptions is limited, conscious behavioural synchronisation [75] or exhibition of the same behaviour by strongly bonded individuals in different species is evident. Synchronisation of activities, like foraging and collective movement, in a multi-level society of feral horses is influenced by dyadic social associations, with higher associations leading to better synchronisation [76]. Stronger affinitive bonds result in more successful spatio-temporal movements in horses, too [77]. Desert baboons follow their friends during the departure phase of collective movements [78]. In addition, microhabitat-level space use patterns, in terms of resting site selection, can be governed by preferential strong social

associations. Cape buffalo and forest buffalo choose specific resting sites (e.g., forest clearing) that enable them to sit in very close proximity to each other (often including body contact) and facilitate social interactions [79–81]. Close spatial associations can foster allopreening in parrots and corvids [82]. These results strongly suggest that preferential social associations can form during foraging, collective movements and resting, and such associations may not necessarily be random and simple by-products of sharing a common space. Therefore, while the general herd-level social associations in space use patterns may strengthen group cohesion and help avoid predators through 'many eyes' [83], preferential social associations or friendships can still be sustained. As evident in a species like water buffalo, where direct affiliative interactions, like allogrooming, are predominantly absent [45], spatial proximity patterns can be of vital importance for maintaining friendships (cf. [46]). Hence, instead of fully relying on the assumption of the "gambit of the group" [84], species-specific 'norms' of friendships can be present, i.e., without necessitating direct affiliative interactions among friends (cf. [20,29,45,46,58]).

Our assessment of buffalo friendships encompassed all aspects of grazing, movement, and resting in dry and wet seasons. The strength of overall observed differential dyadic associations suggests that friendships were likely sustained throughout contexts and climatic conditions. While friendships were age-independent, we could not test the potential effects of kinship. Kinship can govern close social associations potentially mediated through 'familiarity'. Yet, friendships may form both within genetically closely related and unrelated members, suggesting that kinship is not necessarily a prerequisite for the emergence of friendships [12,20,29]. Additionally, dominance rank differences did not predict friendships in buffalo. In highly despotic societies with steep dominance hierarchies, rank-based cooperation among group members or selectivity in benefiting group members is evident [12,85]. The low to moderate steepness values in dominance hierarchies in female buffalo might explain why rank differences are not suitable drivers of friendships.

Personality traits in buffalo

Using an objective bottom-up method, we reported three personality traits in feral buffalo: social tension, vigilance, and general dominance. While these personality traits are subjectively labelled (cf. [30,42,47–50]), the underlying repeatable behaviours may have crucial socio-ecological implications for buffalo. The social tension trait consisted of three behaviours: *approach*, *self-groom*, and *avoid*. Approaching a conspecific or even heterospecific and tolerating them is interpreted as the tendency to be sociable [86], which has substantial adaptive implications (see [44] for a detailed discussion). Self-groom, or broadly, self-directed behaviour in animals, is a widely used indicator of stress-related responses,

contributed by social (e.g., hierarchical group structure) or non-social (e.g., presence of ectoparasites) factors [48,87–89]. Finally, avoiding (specific) conspecifics can be attributed to the hierarchical social structure of buffalo (see [90]), which may help reduce conflicts, competition and disease transmission within the herd [91]. However, counterintuitively, approach behaviour positively co-varied with self-groom and avoidance (of conspecifics), indicating aspects of both sociability and tension. The availability of partners, space, and distribution of food resources in social and ecological niche can potentially explain why behaviours of two different extremes may have positively co-varied [92]. In other words, individuals may show consistent behavioural 'tactics' to fulfil their social and ecological needs.

The second buffalo personality trait, vigilance, was labelled after the only behavioural variable loaded in it. Vigilance, in general, has a high adaptive value associated with predator avoidance, however, our study population of feral buffalo has no natural predators. Thus, proximately, this behaviour can be attributed to focusing on within-herd events, like ongoing physical fights, or paying attention to nearest neighbours [93]. In addition to resident males within the herds, other territorial males who were not part of the observed herds were present in the study area. Subsequently, frequent territorial fights among resident and non-resident males, often followed by female guarding, were observed (personal observations, D.B., 2023-2024). The approach of the resident male for mate guarding can make nearby females vigilant. However, individuals who are not within a guarding radius can avoid being vigilant. Further, individuals with relatively low dominance ranks can collect spatiotemporal information on aversive events (like fights and aggression) and nearest neighbours (like an approaching male or other higher-ranking herd members) and benefit by escaping or avoiding conflicts. Therefore, even in the absence of natural predators, consistent variations in vigilance behaviour in feral buffalo can provide substantial benefits.

The third and final personality trait of buffalo, general dominance, has two inversely co-varying behaviours, *sit* and *displace*. General dominance is often linked to boldness and exploration [94] (but see [95]), which are highly beneficial traits when predator pressure is low or absent. In contrast, individuals with low general dominance scores can benefit by avoiding potential conflicts and aggressive interactions. General dominance has further been reported as a manifestation of leadership behaviour in animals [96], which could be useful for decision-making, e.g., in collective movements. To what extent variations in general dominance represented the dominance hierarchy of the herds remains to be investigated, which could not be assessed in this study to avoid data dependence.

Personality homophily and friendships

As hypothesised, we found evidence that personality homophily is a behavioural decision rule of friendship in female water buffalo. Social tension and general dominance, but not vigilance, predicted the preferential strong social associations. Unlike vigilance, social tension and general dominance are social personality traits (i.e., traits that include social interactions [97]). In general, social personality traits, like extraversion and agreeableness, are known to foster friendships and cooperation in humans [98]. Certainly, the buffalo social personality traits do not fully resemble the human social personality traits, yet justification can be made by highlighting the underlying basis of personality homophily: its ability to help form trust and reduce uncertainty among similar individuals [4,21]. Consistent with this idea, similarly (socially-) tensed buffalo can form emotionally mediated attitudes toward herd members through social associations, leading to preferential selection of partners [48,99]. Likewise, differences in general dominance have significant implications for adaptive benefits. A low dominance rank difference or high dominance rank similarity can be associated with better cooperation and coordination [12,100]. Friendships based on similar general dominance status can reduce the monopolisation of resources like food, by facilitating tolerance. In line with previous findings, the non-social vigilance trait did not influence friendships [31], which may suggest that the emergence of friendships in buffalo may depend on social but not on non-social personality traits (but see [29]).

Conclusion

The evolution of social relationships has several complex underpinnings beyond simple demographic characteristics. Using an underrepresented social ungulate species, we provide valuable insights into the proximate mechanisms driving preferential close social relationships or friendships. We identify and discuss the emergence of friendships based on similarities in personalities, a behavioural decision rule which has so far been tested primarily on primates. However, the involved psychological and emotional processes employed for the selection of friends in water buffalo should carefully be assessed before generalising them with that of humans and other non-human primates. Although we highlight the broader evolutionary implications of friendships in buffalo by drawing parallels with other social species, significant gaps in knowledge of feral water buffalo ecology and behaviour have rendered identifying the species-specific norms of sociality and friendships challenging. These limitations call for in-depth investigations to validate how the broad spectrum of ecological relevance pertaining to a host of other taxa aligns specifically with water buffalo.

Data availability

Data and code (R-script) generated from this study will be made available upon publication.

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Authors' contributions

D.B.: conceptualisation, methodology, investigation, data curation, formal analysis, data visualisation, writing—original draft, writing—review and editing; K.J.F.: conceptualisation, funding acquisition, resources, supervision, writing—review and editing; A.G.M.: conceptualisation, funding acquisition, resources, supervision, writing—review and editing. All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

Declaration of interests

We declare that we have no competing interests.

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Figure and figure legend

Figure 1

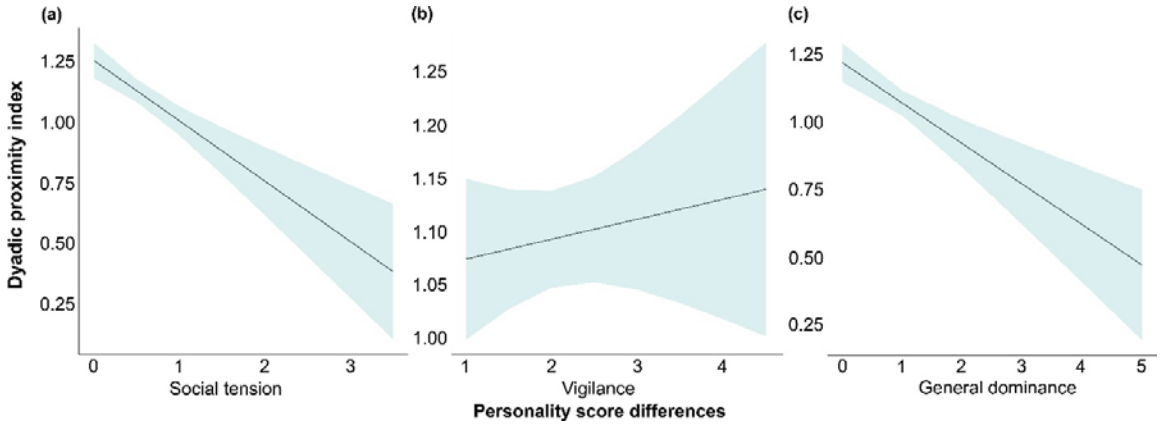

Figure 1 – Effects of buffalo personality score differences on dyadic proximity index. **(a)** GLMM effect plot showing the predicted effect of social tension score differences on dyadic proximity index ($p<0.001$), **(b)** GLMM effect plot showing the predicted effect of vigilance score differences on dyadic proximity index ($p=0.50$), **(c)** GLMM effect plot showing the predicted effect of general dominance score differences on dyadic proximity index ($p<0.001$). Shaded areas in the plots indicate 95% confidence intervals.

Electronic supplementary materials

Table S1 – Details of the study animals. The individual identities, herd memberships, age in years at the beginning of study (June 2023), and dominance ranks are summarised.

Identity	Herd membership	Age in years	Dominance rank
Ross's Mum	Lo Wai Tsuen	19	2
Siu Ying Mum	Lo Wai Tsuen	19	1
Siu Ying	Lo Wai Tsuen	6.5	3
Siu Ying Sis 1168	Lo Wai Tsuen	6	4
Chu 802	Lo Wai Tsuen	10	5
Chu Daughter	Lo Wai Tsuen	6	7
Weak Sister Ping tag	Lo Wai Tsuen	6	6
857	Lo Uk Tsuen	15	23
856	Lo Uk Tsuen	14	20
855	Lo Uk Tsuen	14	18
Ear Pink tag	Lo Uk Tsuen	15	19
Chase Car	Lo Uk Tsuen	12	17
Chase Car Daughter	Lo Uk Tsuen	5	14
Amy's Mum	Lo Uk Tsuen	14	8
Cloud	Lo Uk Tsuen	6	13
1160	Lo Uk Tsuen	6	22
Baby Girl's mum 812	Lo Uk Tsuen	10	21
Baby Girl 1097	Lo Uk Tsuen	5	6
Older Sister 1076	Lo Uk Tsuen	9	1
Younger Sister	Lo Uk Tsuen	9	3
Yellow Button	Lo Uk Tsuen	14	11
Sneaky Boy's mum	Lo Uk Tsuen	15	16
Fighter Girl 1166	Lo Uk Tsuen	4	10
Ah Mui Yellow Button	Lo Uk Tsuen	6	4
1158	Lo Uk Tsuen	8	5
1045	Lo Uk Tsuen	9	7
1159	Lo Uk Tsuen	15	2
No Hair Pink Tag	Lo Uk Tsuen	14	12
1035	Lo Uk Tsuen	11	9
1091	Lo Uk Tsuen	9	15

Table S2 – Ethogram describing the buffalo behaviours and their descriptions. The behavioural categories, names of behaviours, their types and definitions are provided.

Category	Behaviour	Type	Definition
Activity	Walk	State	Individual moves at a regular pace, without ruminating, foraging or grazing and covers at least a three-body length distance.
	Stand	State	Individual stands upright without moving, ruminating, or paying attention to a particular object, event or another individual.
	Sit	State	Individual sits with her head up but without ruminating.
	Lie down	State	Individual lies with one side of the body on the ground. The head position is always down.
	Ruminate	State	Individual chews stored food items with lateral jaw movements, head above mid-line or in line with the body while standing, sitting, or lying.
	Feed	State	Individual places her mouth at the level of grass with clear visible contact. Movement of the mouth can be visible.
	Browse	State	Individual stands with her mouth visibly in touch with plant leaves or shrubs but not grass. Movement of the mouth can be visible.
	Supplement feed	State	Individual feeds on human-provisioned food which are otherwise not part of the natural vegetation, e.g. sweet potato leaves and/or hay.
	Drink	State	Individual places her mouth at the level of water with clearer movements indicative of swallowing water.
	Sleep	State	Individual lies with head down and eyes closed.
	Pass by	Event	Individual enters the radius of one body length of another individual and leaves the radius with the same movement.
	Defecate	Event	Individual releases faeces, usually in a squatting position.
	Urinate	Event	Individual releases urine, often in a semi-squatting position.
	Startle	Event	Individual shows frightened response (frozen body posture with attention towards stimuli) due to a sudden change in the environment (e.g., loud sound, other members moving or loud noises with human artefacts).
	Digging wallow	State	Individual digs soil with her horns and/or hooves with the intention of making a depression to accommodate herself in mud and/or water.
	Wallow	State	Individual is present within a wallow, which

			can happen in conjunction with sitting, lying down, and ruminating.
	Bath	State	Individual is present within a natural waterbody, can happen in conjunction with standing, sitting, lying, and ruminating; the individual can be fully submerged.
Sexual behaviour	Mount	Event	Individual lifts her front side of the body and places it against another individual (usually the hind side of the individual) with two feet off the ground.
	Flehmen	Event	Individual exposes her nostrils and teeth to inhale olfactory cues from another individual; This may pair with lifting the neck and extending the chin with a slightly open mouth and upper lip curled back backwards.
	(Being) Mate	State	Individual mounts and ejaculates, indicated by a pause before dismounting and/or the appearance of visible semen. (For females: Mate is 'being mate' by a male, i.e., a passive behaviour)
	Refusal	Event	Individual leaves or changes position, with or without aggression, while another individual tries to mount.
Social behaviour	Approach	Event	Individual moves toward another individual with clear focus and ends up within their one-body length radius.
	Social rub	State	Individual rubs her body gently on a conspecific's body without displacing the conspecific.
	Social sniff	Event	Individual sucks in the air while holding her head very close to body parts of another individual, except for the genital area.
	Lick	Event	Individual passes tongue or lips over the body of another individual, except the genital area.
	Head touch with head/muzzle	Event	Individual touching the head of another individual with her own head/muzzle.
	Touch other body parts than head with head/muzzle	Event	Individual touching body part except for head of another individual with own head/ muzzle.
	Contact sit or stand (body contact)	State	Individual sits or stands next to another individual with body parts other than horns and limbs touching.
	Contact lie down (body contact)	State	Individual lies next to another individual with body parts other than horns and limbs touching.
	Proximity	State	Individual stays within one body length of another individual.
	Social play	Event	(Either of) Two individuals skip/hop with each other and nuzzle, which do not end in withdrawal.
	Muzzle contact	Event	Individual brings her mouth close to another individual's mouth region.
	Vocalisation	Event	Individual emits vocal sound directed at

			another individual/human/event with head directed towards the point of interest; can also happen during walking.
	Travel together	State	Individual travels parallel to another individual while being within a three body length radius.
	Follow	Event	Individual walks behind another individual in the same direction and stays within a radius of five body lengths. Behavioural synchrony is present.
Agonistic interactions	Displace	Event	Individual causes non-contact movement of another individual away from their previous position, taking at least three steps.
	Avoid	Event	Individual changes her sitting spot or direction while walking to a distance of at least three body lengths from another individual that approaches the focal. Attention of the focal is on the approaching individual.
	Leave	Event	Individual walks away from another individual who is within a radius of one body length.
	Flee	Event	Individual runs away after being approached/chased/lunged at by another individual.
	Freeze	Event	Individual stops displaying body movements (i.e., ear or tail movements) and stands stiff while another individual passes by. Duration is a maximum of 20 seconds(considered another event when exceeds 20 seconds); can happen while being inspected by another individual.
	Physical fight	State	Individuals engages in consistent physical contact with another individual acting to displace the other; the outcome is separation of the two individuals, often with a clear winner.
	Push	Event	Individual forces to change the position of another individual by contact, often with horns.
	Head butt	Event	Individual swings her head with force against the body of another individual.
Self-directed behaviour	Autogroom	Event	Individual licks self with tongue in contact with body, or self-scratches using limbs or inanimate objects such as trees or fence; includes parts such as head, ears, neck, shoulders, back, flanks, rear, legs, belly, and others.
	Head/body shake	Event	Individual rapidly turns the whole body in at least two different directions.
	Yawn	Event	Individual wide opens her mouth and inhales intensely, which can be seen by the expansion of the chest.
	Vigilance	Event	Individual focuses on an event or another individual without body movements for at least three seconds, often exposing nostrils and teeth for inhaling olfactory cues (if

			focusing on an individual).
Interspecific interactions		States and events	Individual directly interacts with a member of a different species (humans, cattle, dogs). Due to the rarity of occurrences, all possible behaviours are pooled.

Figure S1 –

Figure S1 – The spatial positions of females in a feral population of water buffalo. The black rectangle shows two female buffalo sitting in affiliative body contact. The red rectangle shows two female buffalo sitting in proximity (one body length distance). [Photo credit: Debottam Bhattacharjee, Location: Pui O, Hong Kong]

Table S3. Behavioural variables from the buffalo ethogram used in the intraclass correlation analysis and their repeatability measures. Intraclass correlation (ICC (3,1)) analysis output of behavioural variables with their ICC values, 95% confidence intervals (CI) and F- and p-values.

Variables	ICC	95% CI	F-value	p-value
Walk	0.170	-0.197, 0.495	1.410	0.180
Stand	0.241	-0.125,0.549	1.635	0.090
Sit	**0.693**	0.448, 0.841	5.511	<0.001
Lie down	**0.580**	0.284, 0.776	3.765	<0.001
Ruminate	-0.146	-0.477, 0.220	0.745	0.784
Feed	0.499	0.174, 0.725	2.989	0.002
Pass by	0.402	0.055, 0.662	2.344	0.013
Wallow	**0.521**	0.204, 0.739	3.176	0.001
Bath	0.312	-0.048, 0.601	1.907	0.044
Flehmen	**0.722**	0.494, 0.857	6.202	<0.001
Approach	**0.710**	0.474, 0.850	5.886	<0.001
Contact sit	**0.619**	0.338, 0.799	4.250	<0.001
Contact lie down	0.479	0.150, 0.713	2.840	0.003
Proximity	**0.579**	0.282, 0.775	3.754	<0.001
Travel together	**0.554**	0.247, 0.759	3.482	0.001
Displace	**0.601**	0.312, 0.788	4.009	<0.001
Avoid	**0.728**	0.503, 0.861	6.355	<0.001
Leave	**0.592**	0.300, 0.783	3.906	<0.001
Self-groom	**0.850**	0.709, 0.926	12.32	<0.001
Head/Body shake	**0.788**	0.602, 0.893	8.446	<0.001
Vigilance	**0.777**	0.583, 0.887	7.974	<0.001

Variables with ICC values ≥0.5 (highlighted by bold interface) are considered repeatable.

Figure S2 –

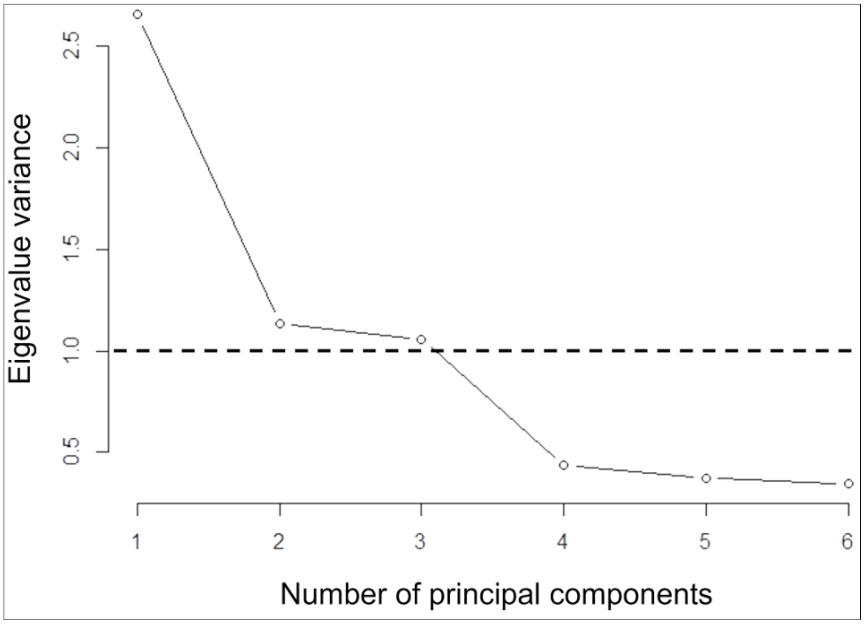

Figure S2 – Screeplot of the principal component analysis to identify buffalo personality traits. The horizontal dashed line indicates the cut-off eigenvalue of '1' for selecting a principal component. Three principal components are selected with eigenvalues >1.

Table S4 – Generalised linear mixed-effect model analysis investigating the effects of buffalo personality- and age- differences on dyadic proximity index.

Model: Dyadic proximity index ~ Social tension difference + Vigilance difference + General dominance difference + Age difference + (1|Individual 1) + (1|Individual 2), family=Gaussian.

	Estimate	**Standard error**	**Z value**	**p-value**
Intercept	1.343	0.049	26.902	<0.001***
Social tension difference	-0.244	0.047	-5.134	<0.001***
Vigilance difference	0.018	0.027	0.672	0.50
General dominance difference	-0.149	0.033	-4.440	<0.001***
Age difference	0.010	0.006	1.483	0.13

Significance code: <0.001 '***'

Table S5 – Generalised linear mixed-effect model analysis investigating the effects of buffalo dominance rank differences on dyadic proximity index.

Model: Dyadic proximity index ~ Dominance rank difference + (1|Individual 1) + (1|Individual 2), family=Gaussian.

	Estimate	**Standard error**	**Z value**	**p-value**
Intercept	1.083	0.034	31.20	<0.001***
Dominance rank difference	-0.004	0.027	-0.166	0.868

Significance code: <0.001 '***'