

Social bonds between unrelated females increase reproductive success in feral horses

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In many mammals, females form close social bonds with members of their group, usually between kin. Studies of social bonds and their fitness benefits have not been investigated outside primates, and are confounded by the relatedness between individuals in primate groups. Bonds may arise from kin selection and inclusive fitness rather than through direct benefits of association. However, female equids live in long-term social groups with unrelated members. We present 4 years of behavioral data, which demonstrate that social integration between unrelated females increases both foal birth rates and survival, independent of maternal habitat quality, social group type, dominance status, and age. Also, we show that such social integration reduces harassment by males. Consequently, social integration has strong direct fitness consequences between nonrelatives, suggesting that social bonds can evolve based on these direct benefits alone. Our results support recent studies highlighting the importance of direct benefits in maintaining cooperative behavior, while controlling for the confounding influence of kinship.

equid | friendship | social structure | alliances | sociality

In mammals, aggressive male behavior has costs for females (1–3), and female avoidance of male harassment has been suggested as an explanation for mating system structure (3–5). For example, in horses, male harassment better explains the unusual harem mating system than resource-based explanations (6). If aggression reduces female fecundity and a counterstrategy involves long-term stable social relationships between females, the formation of affiliative social bonds may be an adaptive strategy. Also, affiliative social interactions have immediate benefits to individuals, such as reduced heart rate in horses (7), reduced stress in guinea pigs and baboons (8, 9), and enhanced immune competence in macaques (10). Therefore, affiliative relationships could have profound impacts on fitness.

The benefits of social bonds can be less immediate than the costs of harassment and, therefore, more difficult to measure (11). Social bonds, sometimes called friendships, have been investigated predominantly in primate societies (12–14), but rarely in other taxa (14), and in most species, same-sex social bonds have only been investigated between relatives (14). Consequently, although the importance of affiliative relationships has been demonstrated (15–17), it is usually not possible to distinguish between the relative evolutionary roles of kin selection and the value of the affiliative relationship per se (12). Bonds between females are subtle and, therefore, less often investigated than aggressive interactions. However, recent research suggests that they are a more important determinant of social structure than previously thought (18, 19). Also, social integration has fitness benefits (15), although no studies have demonstrated its adaptive value in the absence of kinship.

The social system of horses is unusual for ungulates, and similar to some primate species, such as gorilla (20). They live year round in a stable social and breeding group (“band”) consisting typically of one male (although sometimes more than one) (21, 22), one or more unrelated adult females, and their

immature offspring (23). Both male and female offspring disperse from their natal band (20, 24), such that band members are not closely related, and yet breeding group membership is very stable. Band membership is so stable that some females live in the same group for most of their adult lives. Also, horses have a fine-scaled ability to recognize other individuals, similar to highly social primates (25). Therefore, the social bonds between females can be investigated without the confounding influence of kinship. Groups are also loyal to large undefended home ranges that overlap largely or entirely with other groups’ ranges and with bachelor males such that habitat quality varies little between groups (26).

The relative uniformity of the social structure irrespective of ecological conditions, demographic structure, predation risk, and management conditions means that feral horse populations adhere to this social structure globally (23). Mares suffer harassment from both other mares and from stallions, which results in lowered reproductive success. Mares not loyal to a breeding group suffer the highest rate of harassment and are generally in poorer condition, with low reproductive success (6). Consequently, the band structure in horses would usually protect mares from high levels of stallion harassment, and Linklater et al. (6) have suggested that affiliative relationships between mares and other mares or stallions may increase reproductive success by reducing harassment. Social interactions are important for horses, and affiliative relationships are strong and enduring (27, 28), often involving preferred partners or friends (28) who allogroom and stay close while resting (29–31).

In this study, we investigated the impact of social integration or bonding, indexed by allogrooming and spatial relationships, on reproductive success of feral horse mares. Also, we tested whether social integration is related to harassment by stallions and, thus, might form a strategy to reduce reproductive costs associated with harassment.

Results

The composite social integration score was a significant predictor of foals born (multiple regression $F_{6,48} = 10.25$, $r^2 = 0.51$, $P < 0.0001$; Fig. 1, Table 1), but not of foal survival (multiple regression $F_{6,48} = 1.46$, $r^2 = 0.15$, $P = 0.21$; Table 1), although the social integration score was a significant predictor of foal survival independently (Table 1). None of the other variables investigated were significant. However, there was a significant difference in foaling success between bands with a single and multiple stallions ($t_{53} = 2.00$, $P = 0.05$), but not for foal deaths ($t_{53} = 1.16$, $P = 0.25$).

The social integration score was significantly correlated with the rate of harassment, with harassment increasing with decreasing strength of social integration ($F_{1,54} = 11.72$, $P = 0.001$, $r^2 =$

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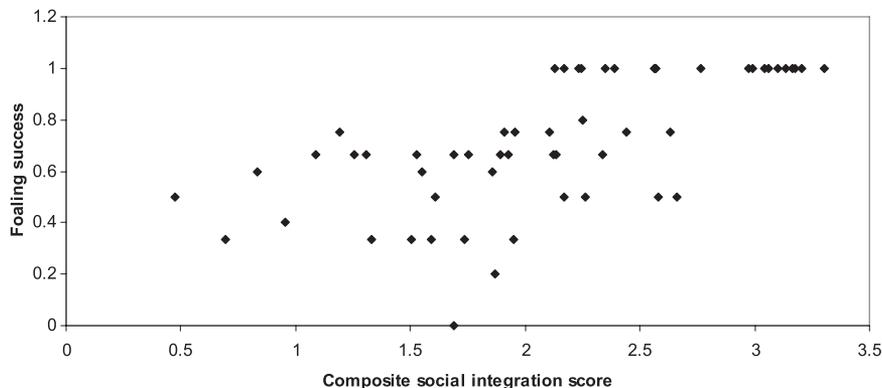


Fig. 1. Effects of social integration on foaling rate for 56 Kaimanawa wild horse mares (1994–1997). Social integration was calculated as the cumulative deviation of a female from the population median for (i) the proportion of time spent close (less than two body lengths) to other mares, proportion of approaches between the focal mare and other mares that were due to the focal mare; and (ii) the proportion of allogrooming events initiated by the focal mare (initiated per initiated plus received). Higher scores represent mares that strongly integrated, whereas low scores represent mares with weaker social bonds.

0.18; Fig. 2), suggesting that social integration may decrease harassment. Although the relationship was largely driven by the females with the lowest social integration scores, the relationship remained significant even if we excluded the four lowest scoring mares (with scores <1 ; $F_{1,50} = 4.63$, $P = 0.04$, $r^2 = 0.08$). Also, foaling rate decreased with increased harassment ($F_{1,53} = 12.91$, $r^2 = 0.18$, $P < 0.001$), but this relationship disappeared when we controlled for social integration (residual analysis $F_{1,53} = 0.43$, $r^2 = 0.01$, $P = 0.52$).

Discussion

Mare social integration was a significant predictor of reproductive success, possibly acting by reducing harassment. Despite previously reported variation in birth rate and offspring survival between individual mares in this population in relation to age (32) and band type (33), such variation was not found among our smaller sample of focal mares. Also, social integration did not vary with mare age, band type, or dominance. The youngest mares are still in the process of dispersal and have yet to develop band fidelity (20), and therefore, most of these females were excluded from our analysis, because we used only mares with a stable band affiliation. Much of the variation due to age is due to the low rates of reproduction in the youngest mares (32). Band type influenced foaling success, confirming our previous research that showed that mares in multi-stallion bands are more protective of their foals than mares in single-stallion bands, possibly due to the risk of infanticide (33), and that they have lower reproductive success (6). Infanticide of nonpaternal offspring has been reported in the harem-dwelling equids (34–36), including feral horses (37), and in multi-stallion bands, where at least one stallion is not the father of each foal (33). Our study confirms the important role of male harassment on female sociality (6), which we show can be reduced through social integration with other females.

Table 1. Relationship between mare social characteristics and foal birth rates and survival

Variables	β (birth)	β (survival)
Composite social integration score	0.65**	0.29*
Time spent allogrooming	−0.01	0.02
Dominance	−0.03	0.06
Age	0.20	0.04
Maternal body condition	0.15	0.10
No. of stallions in band	−0.16	0.22

*, $P < 0.05$; **, $P < 0.0001$.

Therefore, our data show that social integration increases reproductive success among unrelated nonprimate mammals. These results are consistent with findings on primates (15) between related females (16, 17, 38). Females benefit directly by reducing harassment received, and harassment reduces reproductive success in horses (6) and other mammals (2, 39, 40). Additional benefits could include reduced stress levels (41), because harassment increases stress levels and decreases body condition (6). Social contact itself may also decrease stress, and grooming has physiological calming effects in horses (7), and social contact has similar effects in other species, including humans (8, 9, 42, 43). Social integration may also explain some conservation successes and failures, because reintroductions are more successful when familiar individuals are translocated (44).

Our study shows previously undescribed fitness benefits to social integration in the absence of kinship in nonhuman mammals. Therefore, inclusive fitness benefits are not necessary to explain the evolution of such bonds. Recent studies have highlighted the importance of direct benefits in cooperative relationships (45–47), and our study supports these conclusions while controlling for the confounding influence of kinship. In humans, friendships with nonkin increase long-term indicators of reproductive success, such as longevity (42). However, short-term benefits to social contact not only occur between nonrelatives, but even between species; human contact reduces stress in a range of domestic species (42), and human stress may be decreased by contact with domestic pets (42, 48).

Consequently, social bonding between individuals, although difficult to measure, is an important and overlooked contributor to individual variation in lifetime reproductive success in many species, including humans. Studies of group-living in mammals should consider not only group size and composition, but the affiliative relationships between individuals within groups.

Methods

We studied the social relationships of feral horses in the south western Kaimanawa ranges in the North Island of New Zealand, as part of a detailed study of social structure and parental care (21, 26, 33, 49). Horses had been feral and largely unmanaged in this area since the mid 1800s. Kaimanawa horse bands contained usually 1 stallion (but up to 4) and 1 to 11 mares with their immature predispersal offspring. A more detailed description of the Kaimanawa population can be found elsewhere (26).

Behavioral data were derived from 55 individually identifiable adult mares that belonged to the same band over the study (August 1994 to March 1997). We restricted our study population in this way, because changing bands lowers reproductive success and confounds the friendship-fitness relationship (6, 33), and these mares are likely to still be in the process of dispersing from their natal band (20, 24). All individuals in our study population (>400) were

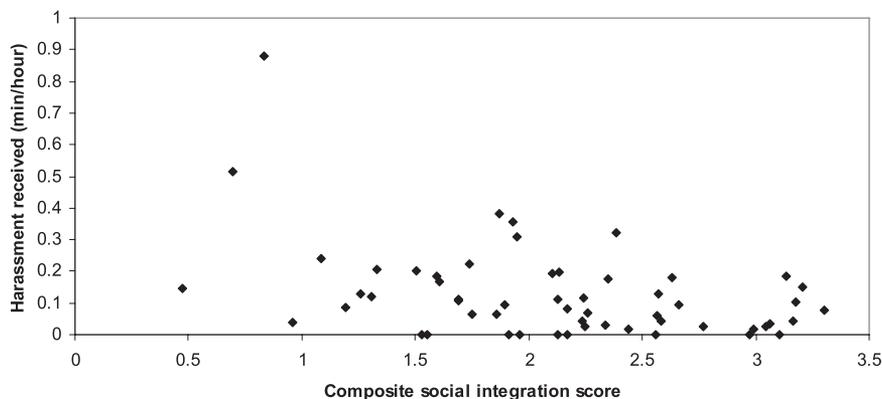


Fig. 2. Effects of social integration on rates of harassment received by 56 Kaimanawa wild horse mares (1994–1997). Social bonding was calculated as the cumulative deviation of a female from the population median for (i) the proportion of time spent close (less than two body lengths) to other mares, proportion of approaches between the focal mare and other mares that were due to the focal mare; and (ii) the proportion of allogrooming events initiated by the focal mare (initiated per initiated plus received). Higher scores represent mares that had stronger social bonds, whereas low scores represent mares with weaker social bonds.

individually identified by either uniquely coded freeze brands on their rumps or by variation in their coat color and, particularly, facial and leg markings. Mares were aged by tooth wear and eruption patterns (50, 51), because mare age can influence reproductive success in horses (31). Aging by tooth wear decreases in accuracy with increasing age (51), and therefore, we classified mares into the following age categories: young (3–5 years, before reaching their full reproductive potential) (52), midaged (6–8 years), and old (at least 9 years) (32, 53). Teeth were examined after horses had been gathered into purpose-built yards and restrained in a hydraulic crush. Mares were also classified into band type on the basis of whether there were 1 or more stallions in a band (single vs. multi-stallion band). Band type has previously been shown to influence foaling success (6, 33).

Bands were located regularly, and mares sampled in focal animal samples (54). Focal sample lasted for at least 1 h, or until a mare moved irretrievably out of view. For mothers, samples could be longer, because they were not terminated until at least three suckle bouts had occurred (or the female moved irretrievably out of view). Samples were evenly distributed throughout daylight hours in all seasons and weather conditions. A total of 2,115 h of focal sample data were collected, averaging 38 h per female. During a focal sample, instantaneous samples (54) were taken every 4 min to record the number and identity of individuals within two body lengths of the focal mare, which we considered to be close (33, 49). During the sample, the following behaviors were recorded on an all-occurrence basis: mutual grooming events between the focal female and any other mares, and all aggressive interactions between the mare and any other adults. The initiator of each event was recorded, and, in the case of aggressive interactions, we also recorded the winner. Also, we recorded every time that a mare was approached by another mare, or approached another mare, to within two body lengths (close) (49). We used these behavioral measures to calculate: (i) the rate of harassment received, calculated as the hourly rate of aggressive events directed at the focal mare; (ii) dominance score, dominance ranks were not comparable across social groups, and so we used a dominance score (interactions won per total interactions) to assign relative ranks; (iii) proportion of time the focal mare spent close to other mares; (iv) proportion of all allogrooming events that were

initiated by the focal mare (initiated per initiated plus received); and (v) approaches, the relative contribution of the focal mare to maintaining contact (to within two body lengths) with other mares (focal mare approached another mare per focal mare approached plus focal mare was approached).

The latter three scores were highly intercorrelated, and so we combined these measures into a composite social integration score based on a similar measure previously used in primates (15, 55). Because social bonds are indicated by spatial proximity and participation in mutual grooming (29–31), we used two measures of the spatial relationship: proportion of time a mare spent close (less than two body lengths) to other mares, and proportion of approaches between the focal mare and other mares that were due to the focal mare, and the proportion of allogrooming events initiated by the focal mare (initiated per initiated plus received). For each measure, we calculated the mare's score, and divided this by the median score for all mares. These scores were summed and divided by 3. Consequently, each measure contributed equally to the data eliminating the possibility that only one of these measures was driving any observed relationships. The calculation followed a previously described equation (15), and yielded a composite measure of social integration.

Mare reproductive success was measured by birth success, and the death rate of foals from birth to 1 year. Individual birth success was determined as the proportion of foals born divided by maximum number of births possible for that mare during the study period, given a constraint of one foal per year. For most mares, four foals were possible, but a few mares were only available to foal in fewer years, either because they died before the completion of the study, or had foals killed by illegal hunting, such that foal survival could not be measured.

Statistical analysis was conducted using R (Version 2.8.1) or Statistica (Version 8), using Generalized Linear Models. All procedures were approved by the Massey University Animal Ethics Committee.

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