Animal Behaviour 85 (2013) 715–725

Contents lists available at SciVerse ScienceDirect

Animal Behaviour

journal homepage: www.elsevier.com/locate/anbehav

Ontogeny and symmetry of social partner choice among free-living yellow-bellied marmots

Jennifer E. Smith [a,b,c,d,*], Lawrance K. Chung [b,d], Daniel T. Blumstein [b,d]

[a] Department of Biology, Mills College, Oakland, CA, U.S.A.
[b] Department of Ecology and Evolutionary Biology, University of California, Los Angeles, CA, U.S.A.
[c] Institute for Society and Genetics, University of California, Los Angeles, CA, U.S.A.
[d] The Rocky Mountain Biological Laboratory, Crested Butte, CO, U.S.A.

ARTICLE INFO

Article history:
Received 1 October 2012
Initial acceptance 14 November 2012
Final acceptance 7 January 2013
Available online 5 March 2013
MS. number: A12-00764R2

Keywords:
affiliation
group living
kin selection
ontogeny
sibling rivalry

Affiliative interactions have important fitness consequences for individuals. Yet, precisely how social roles emerge across ontogeny outside of the context of agonistic interactions is largely unknown, particularly in free-living species of nonprimates. Here we used longitudinal data on yellow-bellied marmots, *Marmota flaviventris*, residing around the Rocky Mountain Biology Laboratory in Colorado, U.S.A., to investigate the development of social partner choice in free-living rodents. We first characterized the symmetry of affiliative interactions between mother–offspring pairs and within cohorts of individuals as they developed across discrete life history stages. Affiliative behaviours generally increased in symmetry such that exchanges became more reciprocal as individuals matured. We then evaluated the extent to which individuals biased their affiliative behaviour towards, and agonistic behaviour away from, genetic relatives. As predicted by kin selection theory, rates of affiliation increased with the degree of relatedness among individuals at all three life history stages. Thus, nepotism emerged within cohorts of newly weaned pups and persisted into adulthood despite prolonged annual separations due to hibernation. Surprisingly, close relatives also exchanged the highest rates of agonistic behaviour. After accounting for the degree of relatedness, rates of affiliative behaviours given and agonistic behaviours received remained positively correlated, suggesting that close affiliates are each other's closest competitors. Thus, although reciprocity of affiliative exchanges within cohorts increased as individuals matured, competition among genetic relatives emerged early in ontogeny and persisted into adulthood. Taken together, these results highlight changes in social roles shown by individuals across ontogeny and shed light on theories of life history and social evolution.

A growing body of empirical work on free-living mammals suggests that affiliative social interactions have important fitness consequences for individuals (Silk et al. 2003, 2010; Weidt et al. 2008; Cameron et al. 2009; Frere et al. 2010; Wey & Blumstein 2012). In particular, we are now starting to understand that the early social environment may have long-lasting effects on behaviours that persist into adulthood (e.g. Maestripieri & Mateo 2009; Champagne 2010). Moreover, balanced relationships characterized by reciprocal exchanges of affiliative behaviours importantly enhance the health and life span of mammals, ranging from humans (House et al. 1998) to rock hyraxes, *Procavia capensis* (Barocas et al. 2011), and laborataory rats, *Rattus norvegicus* (Yee et al. 2008). Nevertheless, precisely how free-living animals make decisions with respect to initiating affiliative behaviours and how symmetric exchanges develop across ontogeny remains elusive. For example, the vast majority of studies focusing on the ontogeny of social roles concentrate on the establishment of dominance relationships based on the outcomes of agonistic interactions (e.g. Walters 1980; Holekamp & Smale 1993; Pereira 1995; Archie et al. 2006; Cafazzo et al. 2010; Huang et al. 2011). Those studies that do focus on the ontogeny of nonaggressive behaviours have traditionally focused on domestic (e.g. Ward et al. 2008; Val-Laillet et al. 2009; Pal 2010) or captive animals (e.g. Ralls et al. 1987; Maestripieri 1994; Terranova et al. 1998; Weidt et al. 2008; Toth et al. 2009a). As such, we lack an understanding of the fundamental processes involved in establishing patterns of affiliation among group-mates, especially among free-living species of nonprimates.

Here we investigated the development of affiliative behaviour in the free-living yellow-bellied marmot, *Marmota flaviventris*, a facultatively social rodent for which a complete pedigree and long-term data on behavioural interactions across three discrete life history stages (pups, yearlings and adults) are available. We first describe the development of social roles between mothers and their offspring and then ask whether genetic relationships predict

---

* Correspondence: J. E. Smith, Department of Biology, Mills College, 5000 MacArthur Blvd, Oakland, CA 94613, U.S.A.
E-mail address: jesmith@mills.edu (J. E. Smith).

0003-3472/$38.00 © 2013 The Association for the Study of Animal Behaviour. Published by Elsevier Ltd. All rights reserved.
http://dx.doi.org/10.1016/j.anbehav.2013.01.008

the degree to which affiliative and agonistic behaviours are exchanged within groups of individuals occupying the same life history stage. Recent studies on this species revealed that 1-year-olds (yearlings) are generally involved in more affiliative interactions than are adults (Wey & Blumstein 2010). None the less, how these patterns emerge at early stages of development (at the pup stage), the extent to which mothers and other genetic relatives shape these patterns and the relationships between affiliative and agonistic interactions across a lifetime remain unclear.

Hypotheses Predicting Asymmetry of Social Roles across Ontogeny

Mother–offspring interactions

We tested predictions derived from parental investment theory to understand the degree to which parent–offspring conflict arises between mothers and their developing offspring (Trivers 1974; Mock & Forbes 1992). Because mothers trade off between current and future reproduction, we expected mothers to ‘disagree’ with offspring about the duration of the period of maternal investment. In mammals, such conflict is expected to emerge around the time of weaning, such that pups are expected to seek nourishment or protection from mothers, and hence initiate a greater proportion of affiliative interactions with mothers than vice versa. As offspring forage independently and approach the start of their own reproductive ‘careers’, theory predicts that they should play a less active role in maintaining affiliative relationships with their mothers than do immature pups. We therefore expected affiliative behaviours between mothers and offspring to become more balanced (increase in symmetry) as developing offspring matured. Because virtually all males but only about half of females disperse as yearlings in yellow-bellied marmots (Blumstein et al. 2009; Armitage et al. 2011), we also predicted mothers to play a more active role in maintaining affiliative interactions with female yearlings than with male yearlings.

Interactions within cohorts

Because sociality enhances fitness in yellow-bellied marmots (Armitage & Schwartz 2000), we next investigated the development of social relationships within cohorts (age-mates) of marmots across each successive life history stage. We focused on the ontogeny of affiliative interactions because age-structured dominance has already been demonstrated for this species; older individuals are socially dominant to younger ones (Huang et al. 2011). If selective partner choice is adaptive (Noë & Hammerstein 1994; Dugatkin & Sih 1995), then we expected newly emerged pups to become more selective in their social choices as they matured. Specifically, we expected the symmetry of affiliative interactions to decline across successive stages as individuals come to understand the relative value of each potential social partner in their group. The overall symmetry of affiliative behaviours might decline if individuals compete for access to the most valuable social partners. Alternatively, if social interactions by immature animals are primarily limited by spatial constraints facing pups that are primarily found at burrows (Armitage 1991), then affiliative exchanges should become more balanced within cohorts after newly recruited animals have ‘introduced’ themselves to their group-mates and become integrated within their group’s social network.

Hypotheses Predicting Relationships between Affiliative and Agonistic Interactions

Kin selection theory predicts that individuals should generally gain inclusive fitness benefits from biasing affiliative behaviours towards and harmful behaviours away from close genetic relatives (Hamilton 1964). This theory should explain maternal behaviour directed towards offspring as well as behaviour directed by individuals of both sexes towards their maternal and paternal relatives. However, the protective value of kinship with respect to curtailing aggression in mammals has recently been called into question (reviewed by Widdig 2007). Alternatively, natural selection might favour selfish behaviours in circumstances during which individuals compete with close relatives through forces such as sibling rivalry (Mock & Parker 1997) or reproductive suppression/competition (Wasser & Barash 1983; Stockley & Bro-Jorgensen 2011). Such competition may give rise to reproductive skew, defined here as the extent to which breeding is monopolized by dominant individuals (Johnstone 2000; Cant 2006). Because there is some evidence of reproductive skew in yellow-bellied marmots (Allainé 2000), individuals might direct aggression towards their close associates, many of whom are also their close genetic relatives, if doing so enhances their own survival and/or reproduction.

Although these hypotheses have been tested extensively in nonhuman primates and social insects, and to a lesser extent in social carnivores (reviewed by Widdig 2007; Hager & Jones 2009; Smith et al. 2010), explicit tests of how affiliative behaviours emerge across discrete life history stages in free-living rodents are generally lacking, with data on eusocial naked mole-rats, *Heterocephalus glaber*, being a notable exception (Jarvis 1981). Moreover, previous rodent studies focused on the frequency of agonistic acts without considering variation in the number of opportunities to attack individuals of various degrees of relatedness (e.g. Kareem & Barnard 1982; Wey & Blumstein 2010, 2012). Previous approaches could potentially yield biased conclusions because close kin (e.g. mother–offspring pairs, siblings) typically spend the most time in close proximity to each other. Additional study is therefore warranted.

METHODS

Study Subjects and Field Site

Yellow-bellied marmots are ground squirrels that occupy geographically distinct areas, called colony sites (Armitage 1991). Colonies of marmots vary in size and may include one or more adult males as well as one to several matrilines of adult females and their immature offspring. Residents therefore vary in their degree of genetic relatedness to each other (Olson et al. 2012). From 2002 to 2011, we monitored individually recognized free-living marmots at colony sites located around the Rocky Mountain Biological Laboratory (RMBL) in Gunnison County, Colorado, U.S.A. The current study was part of a long-term study initiated in 1962 (Armitage 2010). We regularly trapped known individuals in Tomahawk traps set around burrow entrances on a biweekly schedule during the active season. Upon capture, we transferred each marmot into a canvas handling bag to weigh it, sex it and determine its age. We marked individual marmots with eartags and Nyanzol cattle dye and collected a hair sample for DNA analysis at first capture. Marmots were classified into three discrete life history stages, each separated by annual periods of hibernation: pups (<1 year old), yearlings (1 year old) and adults (sexually mature animals, ≥2 years old). Because pups were first observed above ground after weaning (~25 days after birth; Armitage 2003a), recording behavioural development prior to the cessation of nursing was beyond the scope of this field study.

Behavioural Data Collection

From April to September, observers monitored each colony site during times of peak activity in the mornings (0700–1000 hours) and afternoons (1600–1900 hours) on most days using spotting scopes from a distance (20–150 m) to avoid influencing the behaviour of the subjects. At each observation session for a given colony site, we recorded all individuals that were present and the duration of that sampling period. We recorded the initiator and recipient of each social exchange observed within the group (for our full ethogram, see Nowicki & Armitage 1979). Briefly, affiliative interactions included greetings, allogrooming, proximity maintenance and playing. Agonistic interactions were all accounts of aggression and displacements for which the initiator directed aggression towards or actively displaced its recipient. Because we were interested in the ontogeny of social (rather than sexual) partner choice, mounting in the context of mating was excluded from our current analyses.

Data reported here were collected during 9025 h of observation at six main colony sites: (1) Bench, (2) Horse mound, (3) Marmot meadow, (4) Picnic, (5) River and (6) Town. We recorded a total of 23 981 social interactions involving 741 participants, including 394 males and 347 females. Affiliative interactions ($N = 20\,318$) consisted of play ($N = 7880$), greetings ($N = 3907$), allogrooming ($N = 1198$) and proximity maintenance (e.g. sitting in body contact ($N = 1325$), sitting within 1 m ($N = 4402$), foraging together ($N = 1191$) or following each other ($N = 415$)). Of the 3663 agonistic interactions that were observed, 2827 (77.2%) were acts of directed aggression and 836 were characterized by one individual displacing the recipient.

Kinship Assignment

We updated our previously published pedigree for this current study by assigning parentage for newly emerged pups based on DNA from hair samples and 12 microsatellite loci (for details, see Olson et al. 2012). Because of the high degree of inbreeding in this species, we considered all pairwise relationships in our pedigree simultaneously when assigning pairwise coefficients of relatedness (r values, ranging from 0 to 1 reflecting the degree of kinship). For example, in cases where a marmot sired a pup with his adult daughter, the sire–pup pair has an r value of 0.75 (rather than the r value of 0.5 that might expected for parent–offspring pairs in the absence of inbreeding). We therefore used the package Kinship2 v.1.3.3 (Therneau et al. 2011; R v.2.12.2, R Foundation for Statistical Computing, Vienna, Austria) to generate a matrix of pairwise coefficients of relatedness from the updated pedigree. The calculated kinship matrix provided us with continuous measures of genetic similarity. We limited our current data set to those pairs of individuals for which both parents were known.

Directional Consistency (DC) of Affiliative Interactions

We first examined the tendency for the mother to be the initiator in social interactions with her offspring based on her offspring's current sex and life history stage. Then, we asked whether individual marmots become more or less selective in their partner choices across ontogeny. Specifically, we created distinct 'cohorts' for each of the three discrete life history stages (pups, yearlings and adults) occupied by individual marmots born between 2002 and 2010 at each of the six colony sites. We followed each cohort of individuals within the same life history stage for a given colony across a transition from one life history stage to the next (e.g. pups in 2010 to yearlings in 2011). Interactions among adults were followed until adults in each cohort were no longer observed at the study site (due to mortality or dispersal) or the end of this study period, whichever occurred first.

To quantify variation in the symmetry of social exchanges, we calculated the directional consistency (DC) index (van Hooff & Wensing 1987) as: $DC = (H - L)/(H + L)$ for each cohort of individuals. DC is a group-level measure based on the number of times behaviours were performed in the direction of higher frequency within each dyad (H) minus the number of times they occurred in the direction of lower frequency within each dyad (L), divided by the number of times it was performed by all individuals. DC ranges from 0 for completely symmetric (bilateral) exchanges to 1 for completely asymmetric (unidirectional) exchanges within a group of individuals. Since DC is a proportion, it allows for meaningful comparisons between matrices that contain unequal numbers of interactions (Isbell & Young 2002; Archie et al. 2006; Smith et al. 2011). For a detailed example of this calculation, see Appendix A in de Vries et al. (1993).

We applied this formula to calculate all DCs for matrices of affiliative interactions constructed for each (1) cohort for pups that matured into yearlings and (2) cohort for yearlings that matured into adults. Each cohort was limited to individuals that all had the opportunity to interact with each other within each year and colony site of interest. Although some individuals may share spatial proximity with group-mates occupying the same burrow during hibernation (Blumstein et al. 2004), active exchanges of social behaviour were annually interrupted by long periods of hibernation over the winter months (Armitage et al. 2003).

Relationships between Affiliative and Agonistic Interactions

We used partial matrix correlations to test the null hypothesis of no correspondence between affiliative behaviour given (matrix X) and agonistic behaviour received (matrix Y) among marmots. This method accounts for nonindependence among dyads while partialling out (controlling for) the effects of a third variable (e.g. sex or degree of genetic relatedness; matrix Y; Hemelrijk 1990a, b; de Vries 1993). Colony-year was the unit of analysis because colony composition changed dynamically across years due to births, mortality and dispersal.

The fossorial nature of this species made recording the precise amount of time each pair of marmots was simultaneously above ground challenging. We therefore calculated daily rates of behavioural exchanges to adjust counts of behaviours based on the number of daily co-occurrences for each pair of marmots, a measure that was consistently recorded throughout the duration of this 10-year study. Daily rates of behaviours directed by one individual towards the other individual within each dyad were calculated as follows: (number of behavioural interactions directed by a focal individual towards the other member of that dyad/number of days that both members of that dyad were observed above ground together). To correct for potential biases, rates were only based on those days for which each pair was observed together. We investigated the relationships between kinship and rates of behaviour across and within each life history stage.

Statistical Analyses

We built generalized linear mixed models (GLMM) using lme4 (Bates & Maechler 2010) in R v.2.6.2 (R Foundation for Statistical Computing, Vienna, Austria) with a binomial response variable to examine the tendency for the mother to be the initiator within social interactions involving mothers and offspring based on the sex and life history stage of her offspring. In all of our models, we included the random effect of each mother–offspring pair to account for repeated measures on the same individuals. We also included 'colony' and 'year' as random effects and used likelihood ratio tests to determine whether each term significantly improved the fit of each model. We calculated the 'repeatability' of individual and year effects as the percentage of residual variance in the LMM attributed to each of these random effects (Lessells & Boag 1987).

Matrix analyses were conducted in MatMan 1.1 (Noldus Information Technology, Wageningen, The Netherlands; de Vries et al. 1993).

Following Hemelrijk (1990a), we required that all animals within any given behavioural matrix were observed together during the colony-year(s) of interest. This ensured that each pair had the opportunity to engage in either affiliative or agonistic interactions with all other individuals included in that matrix. We also limited all matrix analyses to those colony-years in which at least four individuals were observed in at least one affiliative or agonistic exchange with each other (Hemelrijk 1990a). We calculated 95% confidence intervals (CI) for DCs characterizing groups belonging to each life history stage. Rows and columns of matrices were permutated simultaneously for 10 000 times to assess the significance of each K_r statistic (de Vries 1993). Kendall's tau (τ) reflects the strength and direction of each row-wise correlation (τ values range from -1 to 1).

We used Statistica v.6.1 (StatSoft, Inc., Tulsa, OK, U.S.A.) to analyse data failing to meet assumptions of normality and/or homoscedasticity of variances. We compared means for more than two independent groups using Kruskal–Wallis tests. We also compared means for two independent groups using Mann–Whitney *U* tests and compared means from dependent groups using Wilcoxon signed-ranks tests. We set our alpha to 0.05 for main effects; all two-way interaction terms with alphas of less than 0.25 were retained in our final models.

Ethical Note

All procedures were approved under a UCLA research protocol ARC 2001-191-01 (approved on 13 May 2002 and renewed annually) and under permits issued by the Colorado Division of Wildlife. Live trapping and release of the subjects imposed minimal disturbance to these animals (Smith et al. 2012).

RESULTS

Mother–Offspring Interactions across Ontogeny

Overall, offspring initiated the majority of affiliative mother–offspring interactions. Agonistic interactions between mothers and their offspring ($N = 9$ interactions with pups; 183 interactions with yearlings) were less frequent than affiliative behaviours ($N = 428$ interactions with pups; 940 interactions with yearlings; see Table 1 for sample sizes). Mother–pup aggression was extremely rare, but mothers initiated the majority of agonistic interactions when offspring were yearlings (Fig. 1). The full statistical model revealed these nonadditive effects of interaction type (affiliative or agonistic), offspring sex and offspring life history stage on the extent to which mothers were the participant responsible for initiating interactions with offspring. That is, the type of social interaction in which the mother–offspring pair was involved interacted at least to some degree with both the sex (interaction type*sex: $P = 0.027$) and life history stage (interaction type*life history stage: $P = 0.057$) of their offspring (Table 1, Fig. 1). The random effect of the identity of the mother also explained a significant portion of the overall variance (26.6%) in the tendency for the mother to be the individual responsible for initiating mother–offspring interactions (Table 1); suggesting that inter-individual differences in maternal style might exist among mothers.

To further investigate these nonadditive effects and the random effect of maternal identity (Table 1), we next modelled the effects of offspring sex and life history stage on maternal behaviour separately within the contexts of affiliative and agonistic interactions. Both models included maternal identity as a random effect. As before, mothers were responsible for initiating social interactions to a greater extent when offspring were yearlings than when offspring were pups in separate models predicting either affiliative ($P < 0.001$) or agonistic ($P = 0.004$) interactions. Sex failed to predict patterns of affiliative exchanges because mothers initiated similar proportions of affiliative interactions with male (32%) and female (38%) offspring (Table 1). Although mothers initiated a greater of proportion of agonistic interactions towards female offspring (93%) than towards male offspring (75%), neither the main effects of offspring sex, nor its interaction with life history stage, were statistically significant predictors of agonistic interactions (Table 1). Thus, overall, life history stage was more important than offspring sex in explaining maternal behaviour. That is, mothers rarely fought with pups, but mothers were typically the party responsible for initiating attacks towards yearlings regardless of offspring sex. In contrast, yearlings initiated a greater proportion of affiliative interactions with mothers than did pups.

Table 1

Independent variables predicting the tendency for yellow-bellied marmot mothers to be the initiator in social interactions with their immature offspring

	Estimate±SE	*Z*	*P*
Full model: affiliative and agonistic social interactions*			
(Intercept)	−1.039±0.210	−4.937	<0.0001
Offspring sex (male)	0.035±0.245	0.143	0.8859
Offspring life history stage (yearling)	0.778±0.226	3.444	**0.0006**
Interaction type (affiliative)	1.561±0.842	1.854	0.0637
Sex × stage	−0.177±0.303	−0.584	0.5594
Interaction type × sex	−1.204±0.545	−2.206	**0.0274**
Interaction type × stage	1.467±0.772	1.901	0.0573
Affiliative interactions only†			
(Intercept)	-0.943±0.180	−5.236	<0.0001
Offspring life history stage (yearling)	0.643±0.168	3.820	**0.0001**
Offspring sex (male)	-0.131±0.162	−0.809	0.4185
Agonistic interactions only‡			
(Intercept)	−1.231±2.871	−0.429	0.6682
Offspring life history stage (yearling)	7.580±2.662	2.848	**0.0044**
Offspring sex (male)	−1.697±2.147	−0.791	0.4292

* Including the random effect of individuals involved improved the fit of the model (likelihood ratio test: $\chi^2_1 = 34.4$, $N = 293$ mother–offspring pairs, $P < 0.001$), explaining 26.6% of the variation in maternal behaviour. Data are based on interactions between mothers and their offspring: $N = 1560$ interactions involving 61 mothers with 182 pups ($N = 85$ females and 97 males) and 158 yearlings ($N = 78$ females and 80 males). The random effect of year ($\chi^2_1 = 10.4$, $P = 0.001$) and colony ($\chi^2_1 = 5.7$, $P = 0.017$) also improved the fit of the model, accounting for 3.9% and 1.7% of variation, respectively. *P* values < 0.05 are shown in bold.

† Including the random effect of individuals involved improved the fit of the model (likelihood ratio test: $\chi^2_1 = 27.6$, $N = 279$ mother–offspring pairs, $P < 0.001$), explaining 23.8% of the variation in maternal behaviour. The random effect of year ($\chi^2_1 = 9.9$, $P = 0.002$) also improved the fit of the model, accounting for 3.8% of the variation, while the random effect of colony did not ($\chi^2_1 = 3.8$, $P = 0.052$). Data are based on 1368 affiliative interactions involving 60 mothers with 180 pups ($N = 85$ females and 95 males) and 138 yearlings ($N = 70$ females and 68 males). The effects of life history stage and sex of offspring on mothers was additive in the context of affiliative interactions (interaction: -0.220 ± 0.303, $Z = -0.728$, $P = 0.467$). Significant values ($P < 0.05$) are shown in bold.

‡ Including the random effect of individuals involved significantly improved the fit of the model (likelihood ratio test: $\chi^2_1 = 11.1$, $N = 83$ mother–offspring pairs, $P < 0.001$), explaining 21.3% of the variation in maternal behaviour. However, neither the random effect of year ($\chi^2_1 = 0.803$, $P = 0.370$) nor that of colony ($\chi^2_1 = 1.86$, $P = 0.173$) improved the fit of the model explaining agonistic interactions. Data are based on 192 aggressive interaction involving 31 mothers with 8 pups ($N = 2$ females and 6 males) and 74 yearlings ($N = 36$ females and 38 males). The model was generated from 192 mother–offspring interactions involving 9 aggressive interactions with pups and 183 aggressive interactions with yearlings. The effects of life history stage and sex of offspring on mothers was additive in the context of aggression (interaction: -0.120 ± 5.438, $Z = -0.022$, $P = 0.982$). Significant values ($P < 0.05$) are shown in bold.

Symmetry of Affiliative Interactions across Ontogeny

Overall, two lines of evidence suggest that the symmetry of affiliative behaviour exchanged within cohorts generally increased

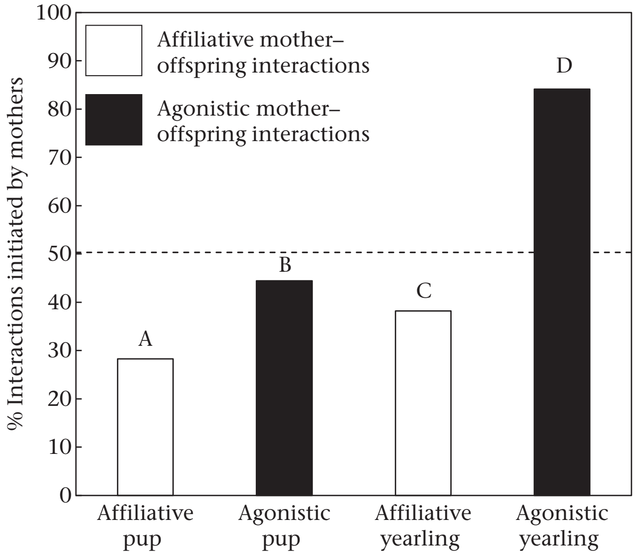


Figure 1. Percentage of social interactions initiated by yellow-bellied marmot mothers involving offspring that were either pups or yearlings. Dashed line represents expected null hypothesis that mothers and offspring were equally responsible for initiating social interactions. Letters above bars indicate statistically significant differences between categories.

as individuals matured. First, DCs of affiliative interactions generally decreased across successive life history stages. Confidence intervals of DCs overlapped with 1 (completely asymmetric) for pups (95% CI = 0.30–1.00, median = 0.66), overlapped with neither 0 or 1 for yearlings (95% CI = 0.16–0.76, median = 0.47), and overlapped with 0 (completely symmetric) for adults (95% CI = 0.00–0.91, median = 0.38). DCs also significantly differed among cohorts of individuals occupying different life history stages (Kruskal–Wallis test: $H_{2,42} = 12.22$, $P = 0.002$; Fig. 2). DCs of affiliative interactions significantly decreased as pups matured into yearlings, suggesting an ontogenetic shift towards more reciprocal exchanges as pups matured into yearlings (Wilcoxon signed-ranks test: $Z = 2.86$, $N = 14$ colony-years, $P = 0.004$). Figure 3 provides an illustrative example of this ontogenetic shift. Symmetry increased within this single cohort of individuals observed at the Horse mound colony first as pups (in 2006) and later as yearlings (in 2007; Fig. 3). Similarly, DCs for matrices containing affiliative interactions involving pups were significantly higher than matrices based on interactions among adults (Mann–Whitney U test: $U = 19.5$, $N = 14$ and 7 colony-years, respectively, $P = 0.028$; Fig. 2). However, DCs of affiliative interactions in matched cohorts of yearlings and adults were statistically indistinguishable (Wilcoxon signed-ranks test: $Z = 0.34$, $N = 12$ colony-years, $P = 0.74$). Taken together, these results indicate that symmetry in affiliative exchanges increased across ontogeny, with adults having the most reciprocal exchanges of affiliative behaviour.

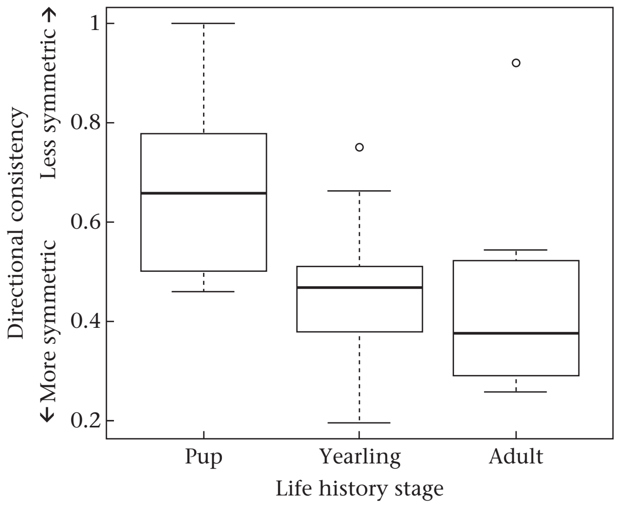


Figure 2. Directional consistency within cohorts of individuals across ontogeny. Dark horizontal lines in box plots represent medians, with boxes spanning the middle 50% of the data for each life history stage. Whiskers stretch to any values that were outside boxes but within the 1.5 interquartile range (IQR) from the median. Circles are outliers, representing values greater than 1.5 IQR away from the median. Values overlapping with 1 were completely asymmetric whereas those overlapping with 0 were completely symmetric.

Degree of Relatedness, Not Sex, Predicts Rates of Behavioural Exchanges

Overall, across all colony-years, the degree of relatedness, but not the sex composition, of social partners involved was positively associated with rates of affiliative and agonistic behaviours exchanged (Table 2; see Supplementary Material, Tables S1 and S2 for the full set of statistical tests). Sex composition of social partners failed to consistently predict rates of interactions for the majority (92%) of the matrices tested (Table S1). Given the weak effects of sex, we focused on the effects of genetic relationships rather than sex in subsequent analyses.

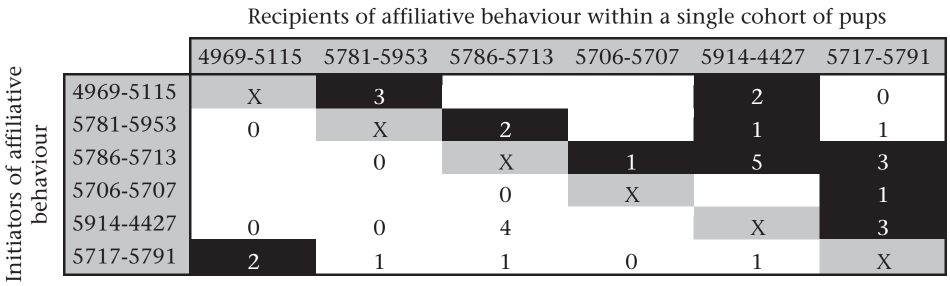
For each colony-year, significant positive relationships emerged between genetic relatedness and the rates at which pairs exchanged either affiliative ($N = 42$ matrices) or agonistic ($N = 42$ matrices) behaviours (Table 2). Similar patterns emerged within each of the three life history stages. As before, close genetic relatives exchanged significantly higher rates of affiliative and agonistic behaviours than did less related pairs within each of the life history stages (Table 3).

Positive Relationships between Affiliative and Agonistic Exchanges

Results at the colony-level indicate that pairs that exchanged the highest daily rates of affiliative behaviours towards colony-mates were most likely to also exchange the highest daily rates of agonistic interactions with each other even after controlling for the effects of genetic relatedness (Table 4; see Supplementary Table S3 for full set of statistical tests). In fact, affiliative behaviours given were significantly associated with the rates at which agonisms were exchanged for all of the colony-years for which sufficient data were available.

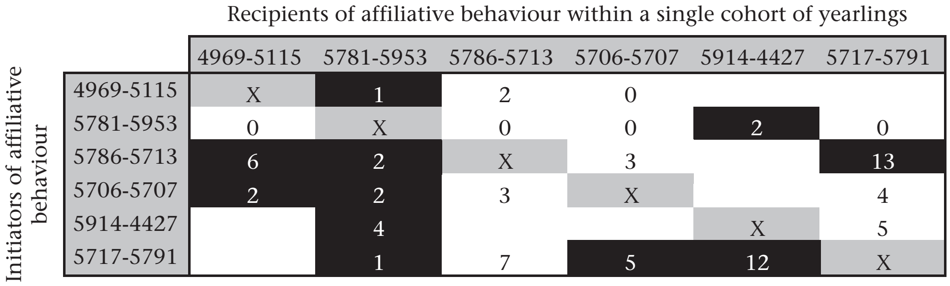
We next investigated relationships among genetic relatedness, affiliative behaviours and agonistic behaviours within each of the three life history stages. As before, we detected positive relationships between affiliative behaviours given and agonistic behaviours received within each of the three life history stages, after accounting for relatedness (Table 5). Interestingly, the proportion of matrix simulations that were statistically significant increased at each successive life history stage. Specifically, only 50% of matrix simulations involving pup–pup interactions were statistically significant (2 out of the 4 colony-years; Table 5). Within yearling cohorts, 68% of matrix simulations involving yearling–yearling interactions were statistically significant (12 out of 18 colony-years, Table 5). Among adults, virtually all (96%) relationships were statistically significant (23 out of 24 colony-years, Table 5). Thus, patterns emerging at the colony level were generally consistent with those found within cohorts at each life history stage, but relationships were most consistent as cohorts matured into adults.

(a) DC = 0.55 in 2006



	4969-5115	5781-5953	5786-5713	5706-5707	5914-4427	5717-5791
4969-5115	X	■ 3			■ 2	0
5781-5953	0	X	■ 2		■ 1	1
5786-5713		0	X	■ 1	■ 5	■ 3
5706-5707			0	X		■ 1
5914-4427	0	0	4		X	■ 3
5717-5791	■ 2	1	1	0	1	X

(b) DC = 0.38 in 2007



	4969-5115	5781-5953	5786-5713	5706-5707	5914-4427	5717-5791
4969-5115	X	■ 1	2	0		
5781-5953	0	X	0	0	■ 2	0
5786-5713	■ 6	■ 2	X	3		■ 13
5706-5707	■ 2	■ 2	3	X		4
5914-4427		■ 4			X	5
5717-5791		■ 1	7	■ 5	■ 12	X

Figure 3. Sample matrices exemplifying the shift in the directionality of affiliative exchanges within a single cohort representing the same six marmots as (a) pups (DC = 0.55) and (b) yearlings (DC = 0.38) at the Horse mound colony in 2006 and 2007, respectively. The rows of the matrix represent the initiator of the interaction and the columns represent those same individuals as recipient of interactions. The identity of each marmot is represented by eight numbers. The intersection of each row and column represent the number of times affiliative interactions were exchanged for each pair. Black squares indicate that one member of the dyad received more interactions than it initiated and white squares indicate dyads for which there were equal numbers of interactions or no interactions (blank) observed. For pups, more dyads exchanged one-way (47%, $N = 7$ dyads) than two-way behaviours (27%, $N = 4$ dyads). For yearlings, fewer dyads engaged in one-way exchanges (33%, $N = 5$ dyads) than in two-way exchanges (40%, $N = 6$ dyads). The same percentages of behavioural exchanges (27%, $N = 4$ dyads) were unknown at both developmental stages.

DISCUSSION

Affiliative Exchanges Increase in Symmetry across Ontogeny

Our results on mother–offspring interactions are generally consistent with the main predictions of parental investment theory (Trivers 1974; Mock & Forbes 1992). That is, affiliative behaviours between mothers and offspring became more balanced as developing offspring matured; this was true regardless of the sex of the offspring. As expected, agonistic interactions were especially rare between mothers and their pups, but mothers were virtually always the party responsible for initiating attacks (~85% of attacks) directed towards yearling offspring. Also as predicted, offspring initiated a smaller proportion of affiliative interactions with their mothers as they matured from pups into yearlings. Interestingly, individual differences in maternal behaviour were repeatable in both agonistic and affiliative contexts. This suggests that mothers possess different maternal styles. This extends similar reports in another free-living rodent, the North American red squirrel, *Tamiasciurus hudsonicus* (Dantzer et al. 2011). Overall, these findings are consistent with the interpretation that dependency of offspring on mothers decreases as offspring mature and that parent–offspring conflict promotes maternal aggression towards yearling offspring just prior to yearlings initiating reproductive ‘careers’ of their own.

Table 2
Relationships between coefficients of relatedness and affiliative or agonistic interactions in yellow-bellied marmots ($N = 42$ colony-years, including a total of $N = 583$ and $N = 616$ marmots, respectively)

	K_r statistic	Kendall's τ	Years (N)	P
Affiliative relationships				
Bench	93±21	0.394±0.071	5 years	≤0.013
Horse mound	30±2	0.560±0.039	2 years	≤0.008
Marmot meadow	392±117	0.408±0.016	9 year	<0.001
Picnic	1043±324	0.508±0.043	10 years	≤0.008
River	452±114	0.371±0.036	10 years	≤0.032
Town	89±13	0.571±0.041	6 years	<0.001
Agonistic relationships				
Bench	94±22	0.449±0.052	5 years	<0.001
Horse mound	26±4	0.621±0.041	2 years	≤0.009
Marmot meadow	257±72	0.412±0.033	9 years	<0.001
Picnic	601±155	0.435±0.039	10 years	≤0.001
River	338±82	0.357±0.056	10 years	≤0.005
Town	84±12	0.612±0.043	6 years	<0.001

K_r: coefficient of relatedness. Kendall's tau (τ) reflects the strength and direction of each row-wise correlation (τ values range from −1 to 1). Because all correlations between genetic relationships and both types of behaviours were statistically significant, summary statistics across years are given as means ± SE for each colony tested (see Supplementary Material, Table S2 for full summary of tests performed for each colony-year).

Our finding that affiliative behaviours within cohorts of marmots increased in symmetry across successive life history stages is inconsistent with the selective partner choice hypothesis. Fine-grained analyses in the future, such as those tracking patterning of partner choice for each specific pair of marmots, are still needed to fully evaluate this notion. Nevertheless, our current finding instead suggests that social interactions by immature animals appear to be primarily limited by spatial constraints facing pups. Newborn pups are virtually always found at their natal burrows (Armitage 1991). Here we show increasingly more balanced affiliative exchanges within cohorts as each member of the cohort

Table 3

Relationships between coefficients of relatedness and either affiliative or agonistic interactions within cohorts of yellow-bellied marmots for which all individuals belonged to one of three life history stages: pups, yearlings or adults ($N = 42$ colony-years, including a total of $N = 583$ and $N = 616$ marmots, respectively)

Life history stage	Colony	Year(s)	Affiliative interactions			Agonistic interactions		
			K_r	Kendall's τ	P	K_r	Kendall's τ	P
Pups	Picnic	**2002**	**318**	**0.299**	**<0.001**	**262**	**0.361**	**<0.001**
(100% of tests statistically significant)	River	**2009**	**46**	**0.302**	**0.006**	**58**	**0.477**	**<0.001**
	Town	**2 years**	**16±4**	**0.67±0.04**	**≤0.042**	**16±4**	**0.76±0.03**	**≤0.039**
Yearlings	Bench	2004	**38**	**0.492**	**<0.001**	**42**	**0.584**	**<0.001**
(92% of tests statistically significant)	Bench	2005	3	0.181	0.248	**12**	**0.722**	**0.042**
	Bench	2007	**28**	**0.244**	**0.035**	**37**	**0.426**	**0.003**
	Bench	2010	**65**	**0.227**	**0.012**	**73**	**0.344**	**<0.001**
	Marmot meadow	5 years	**212±77**	**0.60±0.07**	**≤0.008**	**129±45**	**0.58±0.09**	**≤0.008**
	Picnic	2003	**320**	**0.376**	**<0.001**	**203**	**0.433**	**<0.001**
	Picnic	2006	**354**	**0.280**	**<0.001**	**253**	**0.403**	**<0.001**
	Picnic	2007	**363**	**0.330**	**<0.001**	252	0.000	0.368
	River	2003	**355**	**0.535**	**<0.001**	**327**	**0.499**	**<0.001**
	River	2004	**43**	**0.371**	**0.006**	**34**	**0.427**	**0.003**
	River	2005	9	0.030	0.451	**70**	**0.419**	**<0.001**
	River	2010	**274**	**0.621**	**<0.001**	**138**	**0.520**	**<0.001**
	Town	2 years	**43±13**	**0.70±0.12**	**≤0.001**	**37±7**	**0.68±0.07**	**≤0.001**
Adults	Bench	3 years	**26±6**	**0.58±0.06**	**≤0.029**	**29±3**	**0.73±0.05**	**≤0.003**
(100% of tests statistically significant)	Marmot meadow	5 years	**57±20**	**0.57±0.05**	**≤0.012**	**56±19**	**0.61±0.04**	**≤0.013**
	Picnic	7 years	**351±80**	**0.40±0.05**	**<0.001**	**280±67**	**0.37±0.06**	**<0.001**
	River	7 years	**145±45**	**0.05±0.07**	**≤0.035**	**130±39**	**0.52±0.08**	**≤0.026**
	Town	2 years	**64±4**	**0.53±0.05**	**≤0.001**	**63±1**	**0.54±0.05**	**<0.001**

K_r: coefficient of relatedness. Kendall's tau (τ) reflects the strength and direction of each row-wise correlation (τ values range from −1 to 1). For brevity, when all tests for individuals from a single life history stage within a given colony indicated significant positive correlations, we present associated summary statistics as means ± SE and report the number of years tested. Otherwise, we report the raw results. Bolded rows indicate statistically significant row-wise correlations.

increased its total number of social partners and became more integrated within the overall colony's social network. This finding resembles that found for adult female baboons; social partner stability decreases as the number of potential social partners within the social group increases (Silk et al. 2012). Because marmots may have more opportunities within each day to interact with burrowmates than with members of their colony that occupy different burrows, future studies are therefore needed to understand the degree to which shared microhabitat preferences within each colony site explain social patterns investigated here. Nevertheless, our current study extends earlier research documenting ontogenetic shifts as yearlings mature into adults (Wey & Blumstein 2010). Evaluating daily rates (rather than absolute counts) of behavioural interactions starting at the pup (rather than yearling) stage allowed us to capture early transitions as individuals matured from pups to adulthood. These findings suggest that immature animals play an active, and often underappreciated, role in establishing themselves within their affiliative social networks.

Affiliative interactions became increasingly more symmetric or reciprocal as pups matured into adults; affiliative interactions were asymmetric among pups, moderately symmetric among yearlings, and highly symmetric among adults. These findings are particularly interesting given that outcomes based on wins and losses during play for marmot pups predict their later dominance status as yearlings (Blumstein et al., in press). Increased symmetry across ontogeny for marmots living in colonies structured by nonlinear dominance hierarchies differs from patterns for many species with strict dominance hierarchies. Affiliative behaviours generally become less symmetric as stable dominance relationships emerge (e.g. play in dogs, *Canis lupus familiaris*: Bauer & Smuts 2007; Ward et al. 2008; greetings in spotted hyaenas, *Crocuta crocuta*: East et al. 1993; Smith et al. 2011; agonistic aiding in common ravens, *Corvus corax*: Loretto et al. 2012). Moreover, female macaques (Macaca spp.) are more selective in choosing grooming partners as they mature from infants into adults; macaques form kin-biased networks that resemble, but are differentiated from, those of their mothers (Berman 1982; de Waal 1996; Mondragón-Ceballos et al. 2010). However, ontogenetic shifts in marmots do resemble those of chimpanzees, *Pan troglodytes*. As in marmots, chimpanzee play increases in symmetry as infants mature into juveniles

Table 4

Results of partial row-wise matrix correlations within each colony-year between daily rates of affiliative (matrix X) behaviours given and agonistic (matrix Y) behaviours received by yellow-bellied marmots, after controlling for the effects of genetic relatedness (matrix Z; $N = 42$ colony-years, including a total of $N = 583$ marmots)

Colony	Years (N)	Kendall's τ row-wise correlation				P
		Affiliative (X) vs agonistic (Y)	Affiliative (X) vs kin (Z)	Agonistic (Y) vs kin (Z)	Affiliative (X) vs agonistic (Y) (controlled for kin = Z)	
Bench	5	0.53±0.07	0.39±0.07	0.45±0.05	0.43±0.07	≤0.002
Horse mound	2	0.62±0.09	0.41±0.02	0.41±0.03	0.55±0.11	≤0.007
Marmot meadow	9	0.55±0.05	0.51±0.04	0.44±0.04	0.42±0.04	≤0.007
Picnic	10	0.46±0.03	0.37±0.04	0.36±0.06	0.37±0.01	≤0.048
River	10	0.60±0.04	0.38±0.03	0.39±0.03	0.52±0.05	≤0.002
Town	6	0.68±0.04	0.57±0.04	0.61±0.04	0.51±0.05	<0.001

Kendall's tau (τ) reflects the strength and direction of each row-wise correlation (τ values range from −1 to 1). Because all matrix correlations were statistically significant, summary statistics are represented as means ± SE across years for each colony tested (see Supplementary Material, Table S3 for full summary of tests performed for each colony-year).

Table 5
Results of partial row-wise matrix correlations within each colony-year between daily rates of affiliative behaviours given (matrix X) and agonistic behaviours received (matrix Y) by yellow-bellied marmots, after controlling for the effects of genetic relatedness (matrix Z; $N = 46$ colony-years, including a total of $N = 452$ marmots) within cohorts for which all individuals belonged to one of three life history stages: pups, yearlings or adults

Life history stage	Colony	Year(s)	Kendall's τ row-wise correlation				P
			Affiliative (X) vs agonistic (Y)	Affiliative (X) vs kin (Z)	Agonistic (Y) vs kin (Z)	Affiliative (X) vs agonistic (Y) (controlled for kin = Z)	
Pups (50% of tests statistically significant)	**Picnic**	**2002**	**0.50**	**0.30**	**0.36**	**0.44**	**<0.001**
	River	**2009**	**0.66**	**0.30**	**0.48**	**0.61**	**<0.001**
	Town	2003	0.60	0.63	0.79	0.21	0.147
	Town	2004	0.52	0.71	0.74	0.00	0.481
Yearlings (68% of tests statistically significant)	**Bench**	**2004**	**0.43**	**0.49**	**0.58**	**0.20**	**0.049**
	Bench	2005	0.26	0.18	0.72	0.19	0.202
	Bench	2007	0.16	0.24	0.43	0.07	0.318
	Bench	**2010**	**0.48**	**0.23**	**0.34**	**0.44**	**<0.001**
	Marmot meadow	2003	0.69	0.75	0.80	0.23	0.154
	Marmot meadow	**2004**	**0.60**	**0.61**	**0.41**	**0.48**	**<0.001**
	Marmot meadow	**2007**	**0.44**	**0.40**	**0.43**	**0.33**	**<0.001**
	Marmot meadow	**2007**	**0.37**	**0.51**	**0.49**	**0.17**	**0.024**
	Marmot meadow	2011	0.66	0.75	0.78	0.18	0.133
	Picnic	**3 years**	**0.48±0.02**	**0.33±0.03**	**0.40±0.02**	**0.40±0.03**	**<0.001**
	River	**4 years**	**0.55±0.05**	**0.44±0.09**	**0.47±0.03**	**0.42±0.08**	**≤0.004**
	Town	2004	0.51	0.59	0.62	0.23	0.071
	Town	2005	0.67	0.82	0.75	0.16	0.165
Adults (96% of tests statistically significant)	**Bench**	**3 years**	**0.71±0.07**	**0.58±0.06**	**0.73±0.05**	**0.54±0.08**	**≤0.029**
	Marmot meadow	**5 years**	**0.71±0.03**	**0.57±0.05**	**0.61±0.04**	**0.55±0.06**	**≤0.027**
	Picnic	**7 years**	**0.50±0.05**	**0.40±0.05**	**0.37±0.06**	**0.42±0.03**	**<0.001**
	River	**2002**	**0.73**	**0.72**	**0.78**	**0.38**	**0.021**
	River	2003	0.66	0.80	0.87	-0.09	0.348
	River	**2004**	**0.61**	**0.47**	**0.47**	**0.50**	**<0.001**
	River	**2005**	**0.66**	**0.39**	**0.42**	**0.59**	**<0.001**
	River	**2006**	**0.62**	**0.31**	**0.28**	**0.58**	**<0.001**
	River	**2007**	**0.77**	**0.40**	**0.40**	**0.72**	**<0.001**
	River	**2011**	**0.93**	**0.38**	**0.44**	**0.92**	**<0.001**
	Town	**2 years**	**0.83±0.04**	**0.54±0.04**	**0.54±0.04**	**0.76±0.07**	**<0.001**

Kendall's tau (τ) reflects the strength and direction of each row-wise correlation (τ values range from −1 to 1). Bold values indicate statistically significant results. For brevity, when all tests for individuals from a single life history stage within a given colony indicted significant positive correlations, we present associated summary statistics as means ± SE and report the number of years tested. Otherwise, we report the raw statistical results for each colony-year tested.

(Cordoni & Palagi 2011) and social ranks increase with age (Gilby et al. 2013).

Although comparative data on the DC measure are generally lacking for immature animals, DC values for marmots occupying each of the three discrete life history stages investigated here fall within the ranges reported for adult female mammals. The median DC (0.68) for marmot pups was generally higher than, or similar to, those values for allogrooming in domestic cows, *Bos taurus* (DC = 0.68; Val-Laillet et al. 2009), greetings initiated by spotted hyaenas (DC = 0.65; Smith et al. 2011) and black and white colobus, *Colobus guereza* (DC = 0.60; Kutsukake et al. 2006) as well as those for tail-wagging in wolves, *Canis lupus* (DC = 0.66; van Hooff & Wensing 1987) and friendly approaches in chimpanzees (DC = 0.57; Murray 2007). Median DCs of yearling (0.38) and adult (0.47) marmots most closely resembled those reported for allogrooming in adult female spider monkeys, *Ateles belzebuth hybridus* (DC = 0.51; Leiva et al. 2008), wedge-capped capuchins, *Cebus olivaceus* (DC = 0.43; O'Brien 1993), vervet monkeys, *Cercopithecus aethiops* (DC = 0.33; Seyfarth 1980), and black and white colobus (DC = 0.26; Kutsukake et al. 2006).

Adult exchanges of affiliative behaviours among free-ranging marmots here were more reciprocal and included a wider range of social partners than did immature ones. Social preferences among adults are known to promote stable and equitable social relationships in numerous species of nonhuman primates. For example, balanced exchanges among adult female partners persist over extended periods in baboons (*Papio* spp.: Silk et al. 2006, 2012; Frank & Silk 2009), chimpanzees (Gomes et al. 2009) and tufted capuchins, *Cebus paella* (Schino et al. 2009). Future studies are needed to investigate the extent to which balanced interactions among free-ranging species of nonprimates endure across years.

Nepotism towards Group-mates Persists across a Lifetime

As predicted by kin selection theory, the degree to which pairs of marmots exchanged affiliative behaviours increased with the degree of genetic relatedness. Specifically, our results extend earlier findings suggesting that yearling and adult marmots display a large degree of homophily (Wey & Blumstein 2010), interacting to the greatest extent with age-mates in their social networks with whom they are genetically similar. We additionally reveal here that genetic relationships shape the behaviour of newly weaned pups. Whether yellow-bellied marmots base kin discrimination on past interactions (familiarity), phenotypic matching, or both mechanisms remains unknown. For example, nepotism in Beldings' ground squirrels, *Urocitellus beldingi*, depends upon both forms of information (Holmes 1994; Mateo & Johnston 2000; Mateo 2010). Here we demonstrate a bias in behaviours directed by pups towards their closest relatives and that this nepotism by pups persists into adulthood despite prolonged annual interruptions in social behaviour due to hibernation.

Facultatively social yellow-bellied marmots living in kin-structured matrilines have few unrelated adults with which to interact (Olson et al. 2012). This species therefore differs from many obligately social mammals, which often belong to groups with large numbers of nonkin (e.g. less-related than first-cousins; *r* value < 0.125) as potential social partners. In species such as spotted hyeanas (Smith et al. 2007, 2008), bottlenose dolphins (*Tursiops* sp.: Moller et al. 2001; Gibson & Mann 2008), vervet monkeys (Seyfarth 1980) and chacma baboons, *Papio hamadryas* (Silk et al. 2006, 2012) individuals instead become increasingly selective in their choices of a social partner, fostering individualized social bonds with a relatively small number of group members as they mature into adults.

Costs of Kinship and Affiliating with Group-mates

Although individuals were most likely to direct affiliative behaviours towards their closest genetic relatives, close kin also fought with each other at the highest rates across all three life history stages. These findings fail to support the prediction of kin selection theory that marmots derive net inclusive fitness benefits from withholding aggression from kin belonging to all life history stages. Instead, these patterns are consistent with bodies of theory predicting reproductive competition/suppression among relatives in the forms of sibling rivalry and parent–offspring conflict. Our results are consistent with the notion that close kin are each other's closest competitors; a finding that was particularly striking as marmots matured into adults. Marmots therefore appear to enhance their direct fitness by competing with their closest relatives.

Whereas rates of aggression are inversely related to genetic relatedness in some species of gregarious wasps (Giron et al. 2004; Lize et al. 2012), competition among genetic relatives is apparently prolific. Even though kinship often promotes affiliative behaviours, it provides surprisingly little protection from aggression in zebrafish, *Danio rerio* (Gerlach et al. 2007), house sparrows, *Passer domesticus* (Toth et al. 2009b), meerkats, *Suricata suricatta* (Sharpe & Cherry 2003), European badgers, *Meles meles* (Hewitt et al. 2009), ring-tailed coatis, *Nasua nasua* (Hirsch et al. 2012), and spotted hyaenas (Wahaj et al. 2004; Smith et al. 2010). Similar patterns also persist in numerous nonhuman primates (reviewed by Silk 2002) including ring-tailed lemurs, *Lemur catta* (Kappeler 1993) as well as bonnet macaques, *Macaca radiata,* and rhesus macaques, *Macaca mulatta* (Silk et al. 1981; Bernstein & Ehardt 1986; Widdig et al. 2002). Because intensity rather than the rate of aggression decreases with genetic relatedness in several species including killifish, *Kryptolebias marmoratus* (Edenbrow & Croft 2012), spotted hyaenas (Van Horn et al. 2004) and ringtailed lemurs (Sbeglia et al. 2010), additional data are needed to rule out this possibility for marmots. Nevertheless, our results are particularly interesting because they suggest that close genetic relatives actually direct the highest rates of agonistic behaviour towards kin despite their preferences for these social partners.

Our results also suggest that positive relationships between rates of affiliative and agonistic behaviours existed even after we controlled for the positive effects of kinship on each form of behaviour. Similarly, rhesus macaques direct the highest rates of aggression towards those unrelated social partners with which they associate most often (de Waal 1991, 1986). Such disruptive effects of aggression on relationships within social groups might be limited by the tendency for close associates to reconcile with each other by directing affiliative behaviours towards former opponents (de Waal & van Roosmalen 1979; Aureli et al. 2002). The positive relationship between agonistic and affiliative behaviours found here might be attributed to some extent by reconciliation among valuable social partners. That is, marmots that fight or displace each other most often might also direct affiliative behaviours towards their former opponents as a form of postconflict resolution. Future studies are needed to quantify the precise temporal patterning of agonistic and affiliative exchanges to evaluate this hypothesis.

More generally, our finding that individuals compete at the highest rates with their closest associates is consistent with data on the fitness correlates of sociality in yellow-bellied marmots. Although living in small groups enhances an individual's reproductive success (Armitage & Schwartz 2000), marmots that are least affiliative and most aggressive have the greatest annual reproductive success (Lea et al. 2010; Wey & Blumstein 2010). Reproductive competition might explain these costs; marmots compete for limited burrows to rear young and delay their age of first reproduction beyond that of sexual maturity in the presence of older, dominant females (Wasser & Barash 1983; Armitage 1987, 2003b). Increased risk of attacks by their closest relatives might generate these patterns of reproductive skew. Although mothers virtually never attacked pups in our study, mothers were most likely to be the individuals responsible for initiating agonistic interactions with their young as offspring matured. Maternal aggression could potentially reduce sibling rivalry if mothers intervene on behalf of pups being harassed by their older siblings. Taken together, these results suggest that despite the maintenance of balanced affiliative partnerships among adults, unpredictable aggression directed towards closely related colony-mates might trigger physiological responses that constrain reproduction. Future research is needed to examine this hypothesis in light of viable alternative ones.

Acknowledgments

We thank all the marmoteers who have collected data over the past decade, and especially L.E. Olson, A.J. Lea and M.B. Petelle for parentage assignments. J.E.S. is grateful for postdoctoral fellowships from the American Association of University Women, the Institute for Society and Genetics at the University of California Los Angeles and the American Philosophical Society. L.K.C. is grateful for the support of the Holmes O. Miller Endowment Fund and the Irving and Jean Stone Research Award. D.T.B. was supported by the National Geographic Society, UCLA (Faculty Senate and the Division of Life Sciences), a RMBL research fellowship, and by the National Science Foundation (IDBR-0754247 and DEB-1119660, as well as DBI 0242960 and 0731346 to the RMBL). We thank Dr Nancy G. Solomon as well as two anonymous referees for comments that substantially improved the quality of this manuscript.

Supplementary Material

Supplementary material for this article is available, in the online version, at http://dx.doi.org/10.1016/j.anbehav.2013.01.008.

References

Allainé, D. 2000. Sociality, mating system and reproductive skew in marmots: evidence and hypotheses. *Behavioural Processes*, **51**, 21–34.

Archie, E. A., Morrison, T. A., Foley, C. A. H., Moss, C. J. & Alberts, S. C. 2006. Dominance rank relationships among wild female African elephants, *Loxodonta africana. Animal Behaviour*, **71**, 117–127.

Armitage, K. B. 1987. Social dynamics of mammals: reproductive success, kinship and individual fitness. *Trends in Ecology & Evolution*, **2**, 279–284.

Armitage, K. B. 1991. Social and population dynamics of yellow-bellied marmots: results from long-term research. *Annual Review of Ecology and Systematics*, **22**, 379–407.

Armitage, K. B. 2003a. Marmots: *Marmota monax* and allies. In: *Wild Mammals of North America* (Ed. by G. A. Feldhamer), pp. 188–210. Baltimore: John Hopkins University Press.

Armitage, K. B. 2003b. Reproductive competition in female yellow-bellied marmots. In: *Adaptive Strategies and Diversity in Marmots* (Ed. by R. Ramousse), pp. 133–142. Lyon: International Marmot Network.

Armitage, K. B. 2010. Individual fitness, social behavior, and population dynamics of yellow-bellied marmots. In: *The Ecology of Place: Contributions of Place-based Researcher to Ecological Understanding* (Ed. by I. Billick & M. V. Price), pp. 209–247. Chicago: University of Chicago Press.

Armitage, K. B. & Schwartz, O. A. 2000. Social enhancement of fitness in yellow-bellied marmots. *Proceedings of the National Academy of Sciences, U.S.A.*, **97**, 12149–12152.

Armitage, K. B., Blumstein, D. T. & Woods, B. C. 2003. Energetics of hibernating yellow-bellied marmots (*Marmota flaviventris*). *Comparative Biochemistry and Physiology*, **134**, 103–116.

Armitage, K. B., Van Vuren, D. H., Ozgul, A. & Oli, M. K. 2011. Proximate causes of natal dispersal in female yellow-bellied marmots, *Marmota flaviventris*. *Ecology*, **92**, 218–227.

Aureli, F., Cords, M. & van Schaik, C. P. 2002. Conflict resolution following aggression in gregarious animals: a predictive framework. *Animal Behaviour*, **64**, 325–343.

Barocas, A., Ilany, A., Koren, L., Kam, M. & Geffen, E. 2011. Variance in centrality within rock hyrax social networks predicts adult longevity. *PLoS One*, **6**, 1–8.

Bates, D. & Maechler, M. 2010. Linear mixed-effects models using S4 classes. In: *R Package.* Version 0.999375-33. Vienna, Austria: R Foundation for Statistical Computing, http://lme4.r-forge.r-project.org/.

Bauer, E. B. & Smuts, B. B. 2007. Cooperation and competition during dyadic play in domestic dogs, *Canis familiaris*. *Animal Behaviour*, **73**, 489–499.

Berman, C. M. 1982. The ontogeny of social relationships with group companions among free-ranging infant rhesus monkeys I. Social networks and differentiation. *Animal Behaviour*, **30**, 149–162.

Bernstein, I. S. & Ehardt, C. 1986. The influence of kinship and socialization on aggressive behaviour in rhesus monkeys (*Macaca mulatta*). *Animal Behaviour*, **34**, 739–747.

Blumstein, D. T., Wey, T. W. & Tang, K. 2009. A test of the social cohesion hypothesis: interactive female marmots remain at home. *Proceedings of the Royal Society B*, **276**, 3007–3012.

Blumstein, D. T., Im, S., Nicodemus, A. & Zugmeyer, C. 2004. Yellow-bellied marmots (*Marmota flaviventris*) hibernate socially. *Journal of Mammalogy*, **85**, 25–29.

Blumstein, D. T., Chung, L. K. & Smith, J. E. In press. Early play may predict later dominance relationships in yellow-bellied marmots (*Marmota flaviventris*). *Proceedings of the Royal Society B*.

Cafazzo, S., Valsecchi, P., Bonanni, R. & Natolib, E. 2010. Dominance in relation to age, sex, and competitive contexts in a group of free-ranging domestic dogs. *Behavioral Ecology*, **21**, 443–455.

Cameron, E. Z., Setsaas, T. H. & Linklater, W. L. 2009. Social bonds between unrelated females increase reproductive success in feral horses. *Proceedings of the National Academy of Sciences, U.S.A.*, **106**, 13850–13853.

Cant, M. A. 2006. A tale of two theories: parent–offspring conflict and reproductive skew. *Animal Behaviour*, **71**, 255–263.

Champagne, F. A. 2010. Epigenetic influence of social experiences across the lifespan. *Developmental Psychobiology*, **52**, 299–311.

Cordoni, G. & Palagi, E. 2011. Ontogenetic trajectories of chimpanzee social play: similarities with humans. *PLoS One*, **6**, e27344.

Dantzer, B., McAdam, A. G., Palme, R., Humphries, M. M., Boutin, S. & Boonstra, R. 2011. Maternal androgens and behaviour in free-ranging North American red squirrels. *Animal Behaviour*, **81**, 469–479.

Dugatkin, L. A. & Sih, A. 1995. Behavioral ecology and the study of partner choice. *Ethology*, **99**, 265–277.

East, M. L., Hofer, H. & Wickler, W. 1993. The erect 'penis' as a flag of submission in a female-dominated society: greetings in Serengeti spotted hyenas. *Behavioral Ecology and Sociobiology*, **33**, 355–370.

Edenbrow, M. & Croft, D. P. 2012. Kin and familiarity influence association preferences and aggression in the mangrove killifish *Kryptolebias marmoratus*. *Journal of Fish Biology*, **80**, 503–518.

Frank, R. E. & Silk, J. B. 2009. Impatient traders or contingent reciprocators? Evidence for the extended time-course of grooming exchanges in baboons. *Behaviour*, **146**, 1123–1135.

Frere, C. H., Krutzen, M., Mann, J., Connor, R. C., Bejder, L. & Sherwin, W. B. 2010. Social and genetic interactions drive fitness variation in a free-living dolphin population. *Proceedings of the National Academy of Sciences, U.S.A.*, **107**, 19949–19954.

Gerlach, G., Hodgins-Davis, A., MacDonald, B. & Hannah, R. C. 2007. Benefits of kin association: related and familiar zebrafish larvae (*Danio rerio*) show improved growth. *Behavioral Ecology and Sociobiology*, **61**, 1765–1770.

Gibson, Q. A. & Mann, J. 2008. Early social development in wild bottlenose dolphins: sex differences, individual variation and maternal influence. *Animal Behaviour*, **76**, 375–387.

Gilby, I. C., Brent, L. J. N., Wroblewski, E. E., Rudicell, R. S., Hahn, B. H., Goodall, J. & Pusey, A. E. 2013. Fitness benefits of coalitionary aggression in male chimpanzees. *Behavioral Ecology and Sociobiology*, **67**, 373–381, http://dx.doi.org/10.1007/s00265-012-1457-6.

Giron, D., Dunn, D. W., Hardy, I. C. W. & Strand, M. R. 2004. Aggression by polyembryonic wasp soldiers correlates with kinship but not resource competition. *Nature*, **430**, 676–679.

Gomes, C. M., Mundry, R. & Boesch, C. 2009. Long-term reciprocation of grooming in wild West African chimpanzees. *Proceedings of the Royal Society B*, **276**, 699–706.

Hager, R. & Jones, C. B. 2009. *Reproductive Skew in Vertebrates: Proximate and Ultimate Causes*. Cambridge: Cambridge University Press.

Hamilton, W. D. 1964. The genetical evolution of social behaviour, I and II. *Journal of Theoretical Biology*, **7**, 1–52.

Hemelrijk, C. K. 1990a. Models of, tests for, reciprocity, unidirectionality and other social interaction patterns at a group level. *Animal Behaviour*, **39**, 1013–1029.

Hemelrijk, C. K. 1990b. A matrix partial correlation test used in investigations of reciprocity and other social-interaction patterns at group level. *Journal of Theoretical Biology*, **143**, 405–420.

Hewitt, S. E., Macdonald, D. W. & Dugdale, H. L. 2009. Context-dependent linear dominance hierarchies in social groups of European badgers, *Meles meles*. *Animal Behaviour*, **77**, 161–169.

Hirsch, B. T., Stanton, M. A. & Maldonado, J. E. 2012. Kinship shapes affiliative social networks but not aggression in ring-tailed coatis. *PLoS One*, **7**, 37301–37309.

Holekamp, K. E. & Smale, L. 1993. Ontogeny of dominance in free-living spotted hyaenas: juvenile rank relations with other immature individuals. *Animal Behaviour*, **46**, 451–466.

Holmes, W. G. 1994. The development of littermate preferences in juvenile Belding's ground squirrels. *Animal Behaviour*, **48**, 1071–1084.

van Hooff, J. A. R. A. M. & Wensing, J. A. B. 1987. Dominance and its behavioural measures in a captive wolf pack. In: *Man and Wolf: Advances, Issues and Problems in Captive Wolf Research* (Ed. by H. Frank), pp. 219–252. Dordrecht, The Netherlands: Dr W. Junk.

House, J. S., Landis, K. R. & Umberson, D. 1988. Social relationships and health. *Science*, **241**, 540–545.

Huang, B., Wey, T. W. & Blumstein, D. T. 2011. Correlates and consequences of dominance in a social rodent. *Ethology*, **117**, 573–585.

Isbell, L. A. & Young, T. P. 2002. Ecological models of female social relationships in primates: similarities, disparities, and some directions for future clarity. *Behaviour*, **139**, 177–202.

Jarvis, J. U. M. 1981. Eusociality in a mammal: cooperative breeding in naked mole-rat colonies. *Science*, **212**, 571–573.

Johnstone, R. A. 2000. Models of reproductive skew: a review and synthesis. *Ethology*, **106**, 5–26.

Kappeler, P. M. 1993. Variation in social structure: the effects of sex and kinship on social interactions in three lemur species. *Ethology*, **93**, 125–145.

Kareem, A. M. & Barnard, C. J. 1982. The importance of kinship and familiarity in social interactions between mice. *Animal Behaviour*, **30**, 594–601.

Kutsukake, N., Suetsugu, N. & Hasegawa, T. 2006. Pattern, distribution, and function of greeting behavior among black-and-white colobus. *International Journal of Primatology*, **27**, 1271–1291.

Lea, A. J., Wey, T. W., Martin, J. & Blumstein, D. T. 2010. Heritable victimization and beneficial agonistic relationships. *Proceedings of the National Academy of Sciences, U.S.A.*, **107**, 21587–21592.

Leiva, D., Solanas, A. & Salafranca, L. 2008. Testing reciprocity in social interactions: a comparison between the directional consistency and skew-symmetry statistics. *Behavior Research Methods*, **40**, 626–634.

Lessells, C. M. & Boag, P. T. 1987. Unrepeatable repeatabilities: a common mistake. *Auk*, **104**, 116–121.

Lize, A., Khidr, S. K. & Hardy, I. C. W. 2012. Two components of kin recognition influence parasitoid aggression in resource competition. *Animal Behaviour*, **83**, 793–799.

Loretto, M.-C., Fraser, O. N. & Bugnyar, T. 2012. Ontogeny of social relations and coalition formation in common ravens (*Corvus corax*). *International Journal of Comparative Psychology*, **25**, 180–194.

Maestripieri, D. 1994. Mother–infant relationships in three species of macaques (*Macaca mulatta, Macaca nemestrina, Macaca arctoides*).1. Development of the mother–infant relatinship in the first three months. *Behaviour*, **131**, 75–96.

Maestripieri, D. & Mateo, J. M. 2009. *Maternal Effects in Mammals*. Chicago: University of Chicago Press.

Mateo, J. M. 2010. Self-referent phenotype matching and long-term maintenance of kin recognition. *Animal Behaviour*, **80**, 929–935.

Mateo, J. M. & Johnston, R. E. 2000. Retention of social recognition after hibernation in Belding's ground squirrels. *Animal Behaviour*, **59**, 491–499.

Mock, D. W. & Forbes, L. S. 1992. Parent–offspring conflict: a case of arrested development? *Trends in Ecology & Evolution*, **7**, 409–413.

Mock, D. W. & Parker, G. A. 1997. *The Evolution of Sibling Rivalry*. Oxford: Oxford University Press.

Moller, L. M., Beheregaray, L. B., Harcourt, R. G. & Krutzen, M. 2001. Alliance membership and kinship in wild male bottlenose dolphins *(Tursiops aduncus)* of southeastern Australia. *Proceedings of the Royal Society B*, **268**, 1941–1947.

Mondragón-Ceballos, R., Chiappa, P., Mayagoitia, L. & Lee, P. 2010. Sex differences in learning the allocation of social grooming in infant stumptailed macaques. *Behaviour*, **147**, 1073–1099.

Murray, C. M. 2007. Method for assigning categorical rank in female *Pan troglodytes schweinfurthii* via the frequency of approaches. *International Journal of Primatology*, **28**, 853–864.

Noë, R. & Hammerstein, P. 1994. Biological markets: supply and demand determine the effect of partner choice in cooperation, mutualism and mating. *Behavioral Ecology and Sociobiology*, **35**, 1–11.

Nowicki, S. & Armitage, K. B. 1979. Behavior of juvenile yellow-bellied marmots: play and social integration. *Ethology*, **51**, 85–105.

O'Brien, T. G. 1993. Allogrooming behavior among adult female wedge-capped capuchin monkeys. *Animal Behaviour*, **46**, 499–510.

Olson, L. E., Blumstein, D. T., Pollinger, J. P. & Wayne, R. K. 2012. No evidence of inbreeding avoidance despite survival costs in a polygynous rodent. *Molecular Ecology*, **21**, 562–571.

Pal, S. K. 2010. Play behaviour during early ontogeny in free-ranging dogs (*Canis familiaris*). *Applied Animal Behaviour Science*, **126**, 140–153.

Pereira, M. E. 1995. Development and social dominance among group-living primates. *American Journal of Primatology*, **37**, 143–175.

Ralls, K., Lundrigan, B. & Kranz, K. 1987. Mother–young relationships in captive ungulates: behavioral changes over time. *Ethology*, **75**, 1–14.

Sbeglia, G. C., Tang-Martinez, Z. & Sussman, R. W. 2010. Effects of food, proximity, and kinship on social behaviour in ringtailed lemurs. *American Journal of Primatology*, **72**, 981–991.

Schino, G., Di Giuseppe, F. & Visalberghi, E. 2009. Grooming, rank, and agonistic support in tufted capuchin monkeys. *American Journal of Primatology*, **70**, 101–105.

Sharpe, L. L. & Cherry, M. I. 2003. Social play does not reduce aggression in wild meerkats. *Animal Behaviour*, **66**, 989–997.

Silk, J. B., Alberts, S. C. & Altmann, J. 2006. Social relationships among adult female baboons (*Papio cynocephalus*) II. Variation in the quality and stability of social bonds. *Behavioral Ecology and Sociobiology*, **61**, 197–204.

Seyfarth, R. M. 1980. The distribution of grooming and related behaviours among adult female vervet monkeys. *Animal Behaviour*, **28**, 798–813.

Silk, J. B. 2002. Kin selection in primate groups. *International Journal of Primatology*, **23**, 849–875.

Silk, J. B., Samuels, A. & Rodman, P. S. 1981. The influence of kinship, rank and sex on affiliation and aggression between adult female and immature bonnet macaques (*Macaca radiata*). *Behaviour*, **78**, 111–137.

Silk, J. B., Alberts, S. C. & Altmann, J. 2003. Social bonds of female baboons enhance infant survival. *Science*, **302**, 1231–1234.

Silk, J. B., Alberts, S. C. & Altmann, J. 2006. Social relationships among adult female baboons (*Papio cynocephalus*) II. Variation in the quality and stability of social bonds. *Behavioral Ecology and Sociobiology*, **61**, 197–204.

Silk, J. B., Beehner, J. C., Bergman, T. J., Crockford, C., Engh, A. L., Moscovice, L. R., Wittig, R. M., Seyfarth, R. M. & Cheney, D. L. 2010. Strong and consistent social bonds enhance the longevity of female baboons. *Current Biology*, **20**, 1359–1361.

Silk, J. B., Alberts, S. C., Altmann, J., Cheney, D. & Seyfarth, R. 2012. Stability of partner choice among female baboons. *Animal Behaviour*, **83**, 1511–1518.

Smith, J. E., Memenis, S. K. & Holekamp, K. E. 2007. Rank-related partner choice in the fission–fusion society of spotted hyenas (*Crocuta crocuta*). *Behavioral Ecology and Sociobiology*, **61**, 753–765.

Smith, J. E., Kolowski, J. M., Graham, K. E., Dawes, S. E. & Holekamp, K. E. 2008. Social and ecological determinants of fission–fusion dynamics in the spotted hyaena. *Animal Behaviour*, **76**, 619–636.

Smith, J. E., Van Horn, R. C., Powning, K. S., Cole, A. R., Graham, K. E., Memenis, S. K. & Holekamp, K. E. 2010. Evolutionary forces favoring intragroup coalitions among spotted hyenas and other animals. *Behavioral Ecology*, **21**, 284–303.

Smith, J. E., Powning, K., Dawes, S., Estrada, J., Hopper, A., Piotrowski, S. & Holekamp, K. 2011. Greetings promote cooperation and reinforce social bonds among spotted hyaenas. *Animal Behaviour*, **81**, 401–415.

Smith, J. E., Monclús, R., Wantuck, D., Florant, G. L. & Blumstein, D. T. 2012. Fecal glucorticoid metabolites in wild yellow-bellied marmots: experimental validation, individual differences and ecological correlates. *General and Comparative Endocrinology*, **178**, 417–426.

Stockley, P. & Bro-Jorgensen, J. 2011. Female competition and its evolutionary consequences in mammals. *Biological Reviews*, **86**, 341–366.

Terranova, M. L., Laviola, G., de Acetis, L. & Alleva, E. 1998. A description of the ontogeny of mouse agonistic behaviour. *Journal of Comparative Psychology*, **112**, 3–12.

Therneau, T., Atkinson, E., Sinnwell, J., Matsumoto, M., Schaid, D. & McDonnell, S. 2011. *The R Package Kinship2: Pedigree functions. Version 1.3.3.* Vienna: R Foundation for Statistical Computing.

Toth, Z., Bokony, V., Lendvai, A. Z., Szabo, K., Penzes, Z. & Liker, A. 2009a. Whom do the sparrows follow? The effect of kinship on social preference in house sparrow flocks. *Behavioural Processes*, **82**, 173–177.

Toth, Z., Bokony, V., Lendvai, A. Z., Szabo, K., Penzes, Z. & Liker, A. 2009b. Kinship and aggression: do house sparrows spare their relatives? *Behavioral Ecology and Sociobiology*, **63**, 1189–1196.

Trivers, R. L. 1974. Parent–offspring conflict. *American Zoologist*, **14**, 249–264.

Val-Laillet, D., Guesdon, V., von Keyserlingk, M. A. G., de Passille, A. M. & Rushen, J. 2009. Allogrooming in cattle: relationships between social preferences, feeding displacements and social dominance. *Applied Animal Behaviour Science*, **116**, 141–149.

Van Horn, R. C., Wahaj, S. A. & Holekamp, K. E. 2004. Role-reversed nepotism among cubs and sires in the spotted hyena (*Crocuta crocuta*). *Ethology*, **110**, 413–426.

de Vries, H. 1993. The rowwise correlation between two proximity matrices and the partial rowwise correlation. *Psychometrika*, **58**, 53–69.

de Vries, H., Netto, W. J. & Hanegraaf, P. L. H. 1993. Matman: a program for the analysis of sociometric matrices and behavioral transition matrices. *Behaviour*, **125**, 157–175.

de Waal, F. B. M. 1986. Class structure in a rhesus monkey group: the interplay between dominance and tolerance. *Animal Behaviour*, **34**, 1033–1040.

de Waal, F. B. M. 1991. Rank distance as a central feature of rhesus monkey social organization: a sociometric analysis. *Animal Behaviour*, **41**, 383–395.

de Waal, F. B. M. 1996. Macaque social culture: development and perpetuation of affiliative networks. *Journal of Comparative Psychology*, **110**, 1123–1135.

de Waal, F. B. M. & van Roosmalen, A. 1979. Reconciliation and consolation among chimpanzees. *Behavioral Ecology and Sociobiology*, **5**, 55–66.

Wahaj, S. A., Van Horn, R. C., Van Horn, T. L., Dreyer, R., Hilgris, R., Schwarz, J. & Holekamp, K. E. 2004. Kin discrimination in the spotted hyena (*Crocuta crocuta*): nepotism among siblings. *Behavioral Ecology and Sociobiology*, **56**, 237–247.

Walters, J. 1980. Interventions and the development of dominance relationships in female baboons. *Folia primatologica*, **34**, 61–89.

Ward, C., Bauer, E. B. & Smuts, B. B. 2008. Partner preferences and asymmetries in social play among domestic dog, *Canis lupus familiaris*, littermates. *Animal Behaviour*, **76**, 1187–1199.

Wasser, S. K. & Barash, D. P. 1983. Reproductive suppression among female mammals: implications for biomedicine and sexual selection theory. *Quarterly Review of Biology*, **58**, 513–538.

Weidt, A., Hofmann, S. E. & Konig, B. 2008. Not only mate choice matters: fitness consequences of social partner choice in female house mice. *Animal Behaviour*, **75**, 801–808.

Wey, T. W. & Blumstein, D. T. 2010. Social cohesion in yellow-bellied marmots is established through age and kin structuring. *Animal Behaviour*, **79**, 1343–1352.

Wey, T. W. & Blumstein, D. T. 2012. Social attributes and associated performance measures in marmots: bigger male bullies and weakly affiliating females have higher annual reproductive success. *Behavioral Ecology and Sociobiology*, **66**, 1075–1085.

Widdig, A. 2007. Paternal kin discrimination: the evidence and likely mechanisms. *Biological Reviews*, **82**, 319–334.

Widdig, A., Nürnberg, P., Krawczak, M., Streich, W. J. & Bercovitch, F. 2002. Affiliation and aggression among adult female rhesus macaques: a genetic analysis of paternal cohorts. *Behaviour*, **139**, 371–391.

Yee, J. R., Cavigelli, S. A., Delgado, B. & McClintock, M. K. 2008. Reciprocal affiliation among adolescent rats during a mild group stressor predicts mammary tumors and lifespan. *Psychosomatic Medicine*, **70**, 1050–1059.