# Unreciprocated allogrooming hierarchies in a population of wild group-living mammals

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**Running header**: Unreciprocated allogrooming in European badgers

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***Data Availability Statement:*** *Data are provided in the Supplementary Materials.*

**Lay summary:**

Allogrooming (individuals grooming each other) in animal societies can relate to social status, and has been investigated by comparing allogrooming with dominance rank, calculated from aggressive interactions. This, however, ignores the identity of allogrooming partners. We apply dominance hierarchy analyses to allogrooming in groups of wild European badgers, demonstrating the use of a novel method for understanding allogrooming social structures. We detected marginal unreciprocated allogrooming hierarchies, consistent with a social system with seemingly rudimentary structures.

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## Abstract

Allogrooming can relate to social status in mammalian societies, and thus, be used to infer social structure. This relationship has previously been investigated by examining an individual's dominance rank and their total amount of allogrooming. This, however, does not account for the identity of allogrooming partners. We applied a novel approach, calculating the linearity and steepness of unreciprocated allogrooming hierarchies using actor–receiver matrices in European badgers (*Meles meles*) groups. Badgers have relatively unstructured social groups compared to most group-living carnivores and allogrooming in badgers is currently hypothesized to have a hygiene function. We examine whether allogrooming is linked to social status by investigating: 1) the presence, linearity, and steepness of unreciprocated allogrooming hierarchies; 2) the trading of unreciprocated allogrooming for the potential benefit of receiving reduced aggression from dominant individuals; and, 3) whether unreciprocated allogrooming is associated with relatedness. We found weak unreciprocated allogrooming hierarchies, with marginal linearity, steepness overall, and variation between social-group-years. Unreciprocated allogrooming was positively correlated with directed aggression, potentially providing evidence for the trading of allogrooming for reduced aggression. Allogrooming was not correlated with relatedness, possibly due to high relatedness within social groups. Our findings reaffirm that European badgers have a relatively unstructured social system; likely reflecting a relatively simple state of sociality in Carnivores, with little need for hierarchical order. Using actor–receiver unreciprocated allogrooming matrices to test for linearity and steepness of unreciprocated allogrooming hierarchies in other social species will improve knowledge of group social structure.

**Key words**

Unreciprocated allogrooming hierarchies; linearity of hierarchies; steepness of hierarchies; Biological Trade Model; direct aggression; relatedness

## Introduction

Group living is hypothesized to evolve when it provides benefits that enhance an individual's fitness beyond that achievable from living solitarily (Alexander 1974). Social behaviors may then evolve to increase or maintain this group-living benefit; for example, by reducing the cost of increased parasite and disease transmission (Albery et al. 2020) or by generating a social hierarchy within a group to reduce costly competition between group members (Alexander 1974).

Allogrooming is a common behavior in animal societies whereby group members groom one another. In addition to the 'hygienic function' hypothesis (Freeland 1976; Hutchins and Barash 1976), there is also the 'social function' hypothesis (Sparks 1967). There are several possible social functions of allogrooming and these will likely differ between species, as the structure and quantity of allogrooming is likely species specific. Allogrooming may be performed to retain or enhance social bonds between affiliative conspecifics (Stammbach and Kummer 1982; Kimura 1998; Carter and Leffer 2015; Miyazawa et al. 2020) and reduce/appease within-group aggression by more dominant animals (Birkhead 1978; Schino et al. 1990; O'Brien 1993; Baker and Aureli 2000; Schweinfurth et al. 2017). It may also be used by individuals to conciliate relationships after aggressive interactions (de Waal 1984). Meta-analyses, however, are required to understand how widespread or context dependent these social functions of allogrooming are.

As allogrooming can be related to social status in mammalian societies its distribution between individuals can be highly structured (Forand and Marchinton 1989; Singh et al. 2006; Miyazawa et al. 2020). The identification of allogrooming hierarchies and their relationship with dominance hierarchies-defined from dyadic aggression, in which there is a clear looser and winner-can therefore enhance our understanding of group social-organization (Macdonald et al. 2000). Studies have assessed the relationship between social dominance and allogrooming by correlating the total amount of allogrooming an individual gave to, and received from, all group members against the individual’s dominance rank, determined from agonistic interactions (Singh et al. 2006; Tiddi et al. 2012). To fully ascertain the relationship between dominance rank and allogrooming, however, other factors such as the identity of allogrooming partners and allogrooming reciprocation need to be accounted for (Bitetti 1997). As a step towards this, matrices of allogrooming have been analyzed to test for reciprocity in allogrooming (Lazaro-Perea et al. 2004); unreciprocated allogrooming matrices have been correlated with direct aggression matrices (Hewitt et al. 2009); and a social-network approach has been used to evaluate whether grooming is directed towards higher or lower ranking individuals in an agonistic dominance hierarchy (Šárová et al. 2016). Quantifying the linearity (directional consistency of dyadic unreciprocated allogrooming interactions; de Vries 1998) and steepness (slope of normalized David’s scores against rank; de Vries 1998) of unreciprocated allogrooming hierarchies would indicate whether unreciprocated allogrooming is related to an individual’s social status, but has–to our knowledge–not yet been undertaken.

Another useful way to describe and understand allogrooming hierarchies in relation to dominance is the Biological Trade Model (BTM; Noë and Hammerstein 1994; Noë and Hammerstein 1995). The BTM describes a market-based system in which allogrooming is a commodity traded by subordinate individuals for rank-related commodities from more dominant individuals. The BTM predicts that allogrooming is distributed between all group members with the reciprocation of allogrooming dependent on dominance rank, determined from agonistic interactions (Barrett and Henzi 2006). Evidence supporting the BTM has been found in a number of different taxa, including: Norway rats, *Rattus norvegicus*

(Schweinfurth et al. 2017); meerkats, *Suricata suricatta* (Kutsukake and Clutton-Brock 2010) and, most notably, primates, e.g. female chacma baboons, *Papio cynocephalus ursinus* (Barrett et al. 1999), female tufted capuchin, *Cebus apella nigritus* (Tiddi et al. 2012), and male chimpanzees, *Pan troglodytes* (Kaburu and Newton-Fisher 2015). Alternatively, Seyfarth's (1977) model predicts that allogrooming is clustered between individuals of similar rank, and some studies have documented grooming down the hierarchy (e.g. brown capuchin monkeys, *Cebus apella*, Parr et al. 1997). Such inconsistencies within the literature may result from differences in both social and ecological contexts, influenced by resource availability, distribution, and the value of allogrooming as a commodity within different animal groups.

As philopatry between parents and offspring is usually a key component driving group formation, differences in allogrooming behavior may also be influenced by genetic relatedness. This is because allogrooming can play an important role in enhancing social bonds between relatives (Mooring and Hart 1993; Curtis et al. 2003). Within social-groups of rhesus macaques, *Macaca mulatta*, allogrooming subgroups form based on genetic relationships (Sade 1965). Similarly, during the non-mating season Japanese macaques, *Macaca fuscata*, directed greater levels of grooming towards closely related family members (Mehlman and Chapais 1988). Therefore, genetic relatedness is potentially an important factor to consider when analyzing allogrooming hierarchies. Currently most of the allogrooming literature has been derived from observations in primate societies (Kutsukake and Clutton-Brock 2006; Radford and Plessis 2006) and more studies on other taxa are required to discern how generalizable the results from these studies are.

The European badger (hereafter 'badgers'), *Meles meles*, can form large social-groups (mean group size = 11.3, range = 2–29; da Silva et al. 1994) in high-density populations in the UK, Ireland and Sweden, often via the retention of offspring in their natal territory (Macdonald et al. 2008). Badgers display a simple degree of sociality (Woodroffe and Macdonald 1993), exhibiting social tolerance but incomplete territoriality (Ellwood et al. 2017). Social groups of badgers do display context dependent, steep, linear dominance hierarchies based on directed aggression (Hewitt et al. 2009). Badgers could therefore display some form of social structure relating to social rank. Allogrooming is one of the few potentially cooperative behaviors performed by badgers (Stewart and Macdonald 2003; Johnson et al. 2004), along with, allomarking and a low level of alloparental care (Dugdale et al. 2010). Thus, allogrooming provides a promising behavior for understanding aspects of the social structure of badgers. Furthermore, the facultative sociality of the badger makes it an important species when aiming to understand the evolution of simple animal social structures and cooperative behaviors.

During bouts of allogrooming a badger bites deep into the pelage of another individual, likely to remove fleas from body areas that the individual, itself, cannot reach (Stewart and Macdonald 2003). The combination of allogrooming with self-grooming allows coverage of an individual’s whole body (Macdonald et al. 2000). Badgers display reciprocal allogrooming, where both individuals in a dyadic pair perform allogrooming in a tit-for-tat like strategy (Macdonald et al. 2000) and unreciprocated allogrooming, whereby only the initiator performs the behavior and the receiver does not. Thus, allogrooming in badgers has the potential to be related to social status as unreciprocated allogrooming events may be related to an individual’s rank within the group. Currently, only the potential hygienic function of allogrooming in badgers has been discussed in the literature (Macdonald et al. 2000; Stewart and Macdonald 2003). Although allogrooming can be correlated with directed aggression in badgers (Hewitt et al. 2009), no published studies have analyzed unreciprocated allogrooming hierarchies and their relationship with social status.

We redress the above gap in our knowledge on allogrooming in badgers by focusing directly on unreciprocated allogrooming actor-receiver matrices where the identity of both animals was known. Firstly, we test whether unreciprocated allogrooming is linked to social status by utilizing a novel method of investigating the presence, linearity and steepness of unreciprocated allogrooming hierarchies. Secondly, we investigate the potential trading of unreciprocated allogrooming for rank-related benefits (as predicated by the BTM model; Noë and Hammerstein 1994; Noë and Hammerstein 1995), such as greater tolerance from dominant individuals. If allogrooming is traded for greater tolerance, we predict a positive correlation between unreciprocated allogrooming and directed aggression. This is because individuals may perform higher levels of unreciprocated allogrooming towards individuals from whom they received the highest levels of aggression to gain increased tolerance (Henazi and Barrett 1999). Finally, we test whether allogrooming may be involved in enhancing social bonds among relatives (Mooring and Hart 1993). If this is the case, we predict that relatedness will be negatively correlated with unreciprocated allogrooming and positively correlated with reciprocated allogrooming.

## Methods and Materials

*Study location*

The study was conducted in Wytham Woods, Oxford, U.K. (51°46’26N, 1° 19’19W) – a largely deciduous woodland in which the European badger population has been intensively studied since 1987 (Macdonald and Newman 2002). Group borders were mapped once every two years through bait marking (Macdonald and Newman 2002). We analyzed data collected from the following social-group-years: Sunday's Hill (SH: 1995), Pasticks (P: 1995, 2004 & 2005) and Pasticks Outlier (PO: 2004 & 2005). Pasticks Outlier was initially part of the Pasticks group, however, in 2003 they were identified as two distinct social-groups (Hewitt et al. 2009). For social-group-year compositions by sex, see Table 1.

*Collection of individual data*

Badgers were cage-trapped and sedated four times each year in January, June, August and November (Macdonald and Newman 2002). Capture and handling protocols were licensed under the 1992 Badger Act (Natural England: 20104655), and the 1986 UK Animals (Scientific Procedures) Act (Home Office: PPL30/2835). Captured individuals were sedated with an intramuscular injection of, approximately, 0.2ml ketamine hydrochloride per kg body weight (McLaren et al. 2005). Upon first capture each individual was sexed and given an individual tattoo number to allow for future identification. To enable identification, on CCTV footage, individuals were given a unique fur clip mark (Stewart and Macdonald 1997). Blood or guard hair samples were collected for genetic analyses (Dugdale et al. 2007).

*Genetic analyses of hair and blood samples*

DNA was extracted from hair samples using a Chelex protocol (Walsh et al. 1991) and from blood samples via a GFX genomic blood DNA purification kit (Amersham Biosciences, Little Chalfont, UK). Individuals were genotyped at up to 22 microsatellite loci to assign parentage (Dugdale et al. 2007). An estimation of the Queller and Goodnight's (1989) index of relatedness (*R*) was calculated for each badger pair (Dugdale et al. 2008), using Relatedness 5.0.8.

*Observational analysis of social behavior*

Infrared CCTV cameras (Stewart et al. 1997) were set to film all behavioral actions occurring around focal sett entrances during the night. Each year the cameras were set up at two of the three social-groups: SH and P in 1995; P and PO in 2004, and P and PO in 2005. At P, the largest sett, three cameras were positioned to obtain adequate coverage, whereas at SH and PO one camera each was operated in each study year. A total of 11,230 hours of footage over 319 calendar nights (1st of February to the 31st of March each year) were analyzed.

Each reciprocated and unreciprocated allogrooming event was recorded and the initiator and receiver identities were noted from their unique clip marks (Hewitt et al. 2009). All instances in which a badger initiated allogrooming and the receiver did not reciprocate, by performing the behavior, were classed as unreciprocated allogrooming. Reciprocated allogrooming was classified as two individuals grooming one another, with the initial receiver reciprocating grooming before the badgers walked away from each other. Allogrooming events were classed as terminated when both individuals (in the case of reciprocated allogrooming) or the groomer (in the case of unreciprocated allogrooming) stopped grooming and at least one of the badgers moved their leg(s) away from the other. If either badger paused to look around without physically moving their legs and began grooming again this was classed as the same bout. Over the six social-group-years, we observed a total of 1,768 reciprocated and 841 unreciprocated allogrooming events between 234 dyads. A mean of 31% (28–35%, 95% confidence interval) of all allogrooming events per social-group-year were unreciprocated.

Directed aggression was defined as an actor initiating aggression (bite, nip or charge) at a receiver who did not reciprocate the aggression. Directed aggression ended when the dyad moved at least two body lengths apart for at least 20 s (Hewitt et al. 2009).

*Behavioral matrices*

We weighted actor-receiver matrices of allogrooming by the total number of bouts in which both members of each dyad were seen on camera together. A bout was a period of badger activity on camera, terminating when the last badger left the screen and there was no further activity for one minute (Hewitt et al. 2009). This accounted for differences in the amount of time that each dyadic pair was seen on camera, and thus had the opportunity to be observed interacting. The whole matrix was then multiplied by 100 and rounded to whole numbers (Figure S1). We removed from the matrices dyadic interactions with badgers that were not present or not identifiable for the whole filming period (Hewitt et al. 2009), and all dyadic interactions with cubs, as cubs may be too young to reciprocate allogrooming (Macdonald et al. 2000).

*Hierarchical analyses of unreciprocated allogrooming*

Hierarchies can be measured in terms of linearity, an ordinal measurement offering information on the directional consistency of a dyadic interaction (de Vries 1998). A linear hierarchy within a group is derived from dyadic dominance relationships of group members and is dependent on the degree to which dominance within dyads is consistent across triads within the group (de Vries 1995). Linearity implies that the highest-ranking individual is the winner of all dyadic interactions in the group, and that the second highest ranking individual is the winner of dyadic interactions with all other individuals bar the highest ranking, and so on. To investigate the relationship between allogrooming and social status, we tested for a linear hierarchy in each social-group-year unreciprocated allogrooming matrix. Higher ranking individuals were classed as those that received the most, and initiated the least, unreciprocated allogrooming. We used DomiCalc version 14/05/2013 (Schmid and de Vries 2013), which measures the linearity degree of a hierarchy via an unbiased estimate of Landau's (1951) linearity index *h*. This index is deduced from unreciprocated allogrooming receiver/initiator counts, where any null dyads (unknown relationships) were replaced with ties to avoid biasing *h* (Schmid and de Vries 2013). *h* ranges from 1 to 0, with 1 indicating a completely linear hierarchy and 0 indicating a completely non-linear hierarchy. We performed the test for linearity, by randomly generating a linearity index ($h_r$) 10,000 times. Hierarchies were considered linear if $P_{\text{left}} < 0.05$ (where $P_{\text{left}}$ = number of times that $h_r \geq h$, divided by 10,000), and significantly non-linear if $P_{\text{right}} < 0.05$ (where $P_{\text{left}}$ = the number of times that $h_r \leq h$, divided by 10,000). We then tested for an overall significant effect via Fisher's method of combining p-values (Sokal and Rohlf 1994; Hewitt et al. 2009).

We reordered any social-group-year matrix for which linearity was found, using the improved I&SI method (Schmid and de Vries 2013). The I&SI method correlates each order, with minimal I&SI values, with the Combi1 index, via a Spearman's rank correlation analysis. This produces a matrix with the most optimal order of individuals with respect to the hierarchy. Combi1 is a hierarchical combination of the initiator–receiver unreciprocated allogroomer index (subtraction of the number of individuals to which the central individual initiated unreciprocated allogrooming, from the count of individuals who initiated unreciprocated allogrooming with the central individual), and the proportion of receivers relative to the number of determined dyadic receiver relationships (Schmid and de Vries 2013). The highest Spearman's rank correlational coefficient indicates the most optimal order.

Another measure of social hierarchies is hierarchy steepness. Unlike linearity, which is based on binary dyadic dominance relationships and is calculated from the power of symmetry, steepness considers the power of asymmetry via the analysis of cardinal rank measures (de Vries et al. 2006). While linearity of hierarchies measures directional consistency of dyadic interactions, ‘steepness’ calculates the absolute amount by which individuals (of adjacent rank) differ from each other in their total success in winning encounters (de Vries et al. 2006)), i.e. receiving unreciprocated allogrooming. When the absolute differences between adjacently ranked individuals are large the hierarchy is referred to as steep and when these differences are small it is referred to as shallow. Steepness was calculated using matrices of dyadic indices corrected for chance in R 3.4.0 (R Core Team 2017) using steepness 0.2-2 (de Vries et al. 2006). We assessed the significance of unreciprocated allogrooming hierarchy steepness using 10,000 randomizations. We also tested for an overall significant effect via Fisher’s method of combining *P*-values.

When we identified linear or steep unreciprocated allogrooming hierarchies, we tested for a sex effect against both the I&SI rank and David’s scores rank in R 3.4.0 (R Core Team 2017). We first ran a Shapiro-Wilk test and F-test to confirm normality and homogeneity of variance, respectively, and then tested the sex effect in a two-sample t-test. P 2005 only contained two males and was not normally distributed using a Pearson chi-square test in the R package *nortest* 1.0-4, so we tested for a sex effect using a Wilcoxon rank sum test.

*Directed aggression and unreciprocated allogrooming*

We created weighted, social-group-year matrices for directed aggression between dyadic pairs (Figure S2). We correlated matrices of unreciprocated allogrooming and directed aggression, for each social-group-year, via Kendall’s row-wise correlational analysis (*K*r statistic) in MatMan 1.1 (de Vries et al. 1993)

To test the significance of the *Kr* statistic, we performed 10,000 permutations. If badgers are more likely to initiate unreciprocated allogrooming with individuals from whom they receive more directed aggression there will be a significant, positive correlation between the two behavioral matrices. Thus, a positive correlation between unreciprocated allogrooming and directed aggression may indicate that badgers may be trading allogrooming for decreased aggression. We also tested for an overall significant effect via Fisher's method of combining *P*-values.

*Reciprocated and unreciprocated allogrooming*

We correlated the unreciprocated and reciprocated allogrooming matrices, for each social-group-year, and ran 10,000 permutations to assess the significance of Kr statistic in MatMan 1.1.

*Relatedness and allogrooming*

We correlated matrices containing R values (Figure S3) for each dyadic pair against both unreciprocated (Figure S1) and reciprocated (Figure S4) allogrooming matrices, via the *K*r statistic, for each social-group-year. We ran 10,000 permutations to assess the significance of *K*r statistic in MatMan 1.1. A female badger in P 1995, for which we had no genetic data, was removed from the analyses.

## Results

*Unreciprocated allogrooming hierarchies*

In all but one social-group-year (P 2005), unreciprocated allogrooming hierarchies were not significantly linear (Table 2). However, when testing for an overall linearity effect, we found that when excluding the 2004 data (due to non-independence with 2005) there was an overall linearity effect, but not when excluding 2005 data (Fisher's method of combining p-values: $X^2_8 = 18.5$, $P < 0.025$ and $X^2_8 = 12.8$, $P > 0.05$, respectively). No group had a significantly non-linear hierarchy ($P_{left}$, Table 2), and we found no evidence overall for non-linear hierarchies (Fisher's method of combining p-values: $X^2_8 = 2.1$ [excluding 2004] or 2.5 [excluding 2005]; $P > 0.05$).

We reordered the P 2005 matrix (which had a linear unreciprocated allogrooming hierarchy) via the I&SI improved method (Schmid and de Vries 2013) to find the most optimal order of dominance of these linearly ranked individuals. Four different orders with minimal *I&SI* values ($I = 1$ and $SI = 3$) were identified, and 100% of attempts yielded orders with minimal *I&SI*. This indicates that the algorithm is highly likely to have found the true I&SI minimum. The order with the highest Spearman's rank correlational coefficient of 0.98 was considered most optimal. Sex did not have a significant effect on an individual's I&SI rank in the linear P 2005 hierarchy (Wilcoxon rank sum test: $W = 10$, $P = 0.50$).

We then tested the steepness of unreciprocated allogrooming hierarchies (calculated from the absolute differences between adjacently ranked individuals in their overall success of winning unreciprocated allogrooming encounters). In four of the six social-group-years we found steep unreciprocated allogrooming hierarchies (Table 2), with an overall steepness effect (Fisher's method of combining p-values: $X^2_8 = 48.7$ [excluding 2004] or 40.8 [excluding 2005], $P < 0.001$). P 2005, which had a linear hierarchy, also had the steepest hierarchy (Table 2; Figure S5). We found no significant effect of sex on David's scores rank (SH 1995, $t_{12} = 0.27$, $P = 0.79$; P 1995, $t_9 = -0.94$, $P = 0.37$; PO 2004, $t_5 = -0.36$, $P = 0.73$; P 2005, $W = 5$, $P = 0.67$).

*Directed aggression and unreciprocated allogrooming*

Only one social-group-year (PO 2004) had a significantly positive $K_r$ value for unreciprocated allogrooming and directed aggression matrices and another social-group-year (P 2005) had a borderline significant ($P$-value $< 0.051$) positive $K_r$ value (Table 3). However, there was an overall significant effect (Fisher's method of combining p-values: $X^2_8 = 16.9$ [excluding 2004] or 16.6 [excluding 2005], $P < 0.005$).

*Reciprocated and unreciprocated allogrooming*

Unreciprocated and reciprocated allogrooming were positively correlated in all six social-group years (Table 3). Badgers were therefore more likely to perform unreciprocated allogrooming with badgers that also reciprocated allogrooming with them more.

*Relatedness and allogrooming*

We found no significant negative $K_r$ values for unreciprocated allogrooming and relatedness and no significant positive $K_r$ values for reciprocated allogrooming and relatedness (Table 3). We also found no overall significant effect of relatedness on unreciprocated allogrooming (Table 3; Fisher's method of combining p-values: $X^2_8 =$ 5.1 [excluding 2004] or 2.5 [excluding 2005], $P > 0.05$) and no overall significant effect of relatedness on reciprocated allogrooming (Table 3; Fisher's method of combining p-values: $X^2_8 = 6.5$ [excluding 2004] or 7.8 [excluding 2005], $P > 0.05$).

## Discussion

*Unreciprocated allogrooming hierarchies*

We found minimal asymmetries in the direction of dyadic unreciprocated allogrooming, resulting in weak linearity effects. Although there was overall support for linearity and no support for non-linearity in unreciprocated allogrooming, only one of six social-group-years had a significant linear hierarchy, suggesting context dependence. Additionally, there were only small differences in the number of occasions that individuals performed unreciprocated allogrooming along hierarchies (with higher ranked individuals initiating unreciprocated allogrooming less and being the recipients of unreciprocated allogrooming more), resulting in shallow unreciprocated allogrooming hierarchies in four out of six social-group-years. Overall our findings reflect a weak hierarchical structure in unreciprocated allogrooming in badger social groups. Asymmetry in unreciprocated allogrooming is likely context dependent and could result from individuals having different motivations to solicit allogrooming. For example, the stimulus-driven grooming hypothesis (Riek 1962; Willadsen 1980) predicts that individuals with a higher cutaneous irritation will initiate allogrooming more than individuals with a lower ‘itch burden’.

Although hierarchies of unreciprocated allogrooming have not been directly calculated previously, allogrooming has been correlated with dominance rank in other species, primarily primates, e.g. vervet monkeys, *Chlorocebus pygerythrus* (Seyfarth and Cheney 1984), tufted capuchin monkeys (Bitetti 1997) and lion-tailed macaques (Singh et al. 2006), and also domestic cattle, *Bos taurus* (Šárová et al. 2016). In these species, allogrooming is strongly correlated with dominance rank, implying a strong allogrooming hierarchy, which contrasts with the shallow unreciprocated allogrooming hierarchies that we detected in badgers. This contrast could be related to the amount of time that individuals dedicate to allogrooming. Over 44 primate species, primates spend a mean of 5.2% (StDev = 5.0%; range = 0–18.9%) of their daily activity time grooming (Dunbar 1991). Badgers, in comparison, can spend up to 5.6% of their nocturnal activity time grooming (Stewart and Macdonald 2003). The presence and structure of unreciprocated allogrooming hierarchies is likely to be related to differences in social and ecological context. Importantly, data in our study were only collected during the cub-rearing season, and allogrooming may vary across seasons (Macdonald et al. 2000).

The one social-group-year (P 2005) that displayed a linear unreciprocated allogrooming hierarchy also had the steepest hierarchy. As the steepness of the hierarchy increases, the outcome of dyadic encounters becomes more predictable as the probability of the higher-ranking individual receiving more unreciprocated allogrooming increases, leading to increased linearity (Sanchez-Tojar et al. 2017). As the other social-group-years had shallower hierarchies, linearity was therefore more difficult to infer and was not detected using the I&SI method. However, this finding of a significant linear unreciprocated allogrooming hierarchy was an exception to the overall rule in the six social-group-years studied and badger societies still appear to have only a weak social structure.

For both the I&SI and David’s scores method, sex did not significantly affect an individual’s rank, indicating that sex was not a factor affecting unreciprocated allogrooming interactions in P 2005. The rank order of group members in P 2005, produced by the I&SI method and the normalized David’s scores, differed. This is potentially due to the shallowness of the hierarchy, as the reliability of ranking methods changes with the steepness of the hierarchy – when hierarchies are shallow, the David’s scores method is the most reliable, producing rank orders that have the strongest correlation with known hierarchies (Sanchez-Tojar et al. 2017). Thus, the inferred David’s scores rank order is more reliable than the inferred I&SI rank order for P 2005. This difference in rank order, related to the shallowness of the unreciprocated allogrooming hierarchy, perhaps indicates that unreciprocated allogrooming hierarchies are of limited importance in badger social groups.

### *Directed aggression and unreciprocated allogrooming*

We found weak evidence that unreciprocated allogrooming may be a tradable commodity in badgers (as predicted by the BTM). There was a significant correlation of unreciprocated allogrooming with directed aggression in one social-group-year, borderline significance in a second social-group-year, and overall significance. Badgers may, therefore, be more likely to initiate unreciprocated allogrooming with individuals that directed higher levels of aggression towards them. Unreciprocated allogrooming could thus, serve a placatory function, used by subordinates to avert aggressive encounters with more dominant individuals (Baker and Aureli 2000). The trading of allogrooming for the rank-related benefit of increased tolerance, however, is not nearly as evident or pervasive in badger societies as in other species; for example: semi-free-ranging Barbary macaques, *Macaca Sylvanus* (Carne et al. 2011), meerkats (Kutsukake and Clutton-Brock 2006), female primates (Henazi and Barrett 1999) and Bonnet macaques (Silk 1982). Our results may also relate to the stimulus-driven grooming hypothesis (Riek 1962; Willadsen 1980). Badgers with a higher flea burden and cutaneous irritation may make more unsolicited allogrooming attempts. Unsolicited allogrooming could potentially result in directed aggression to the initiator. Alternatively, directed aggression may elicit conciliatory allogrooming (de Waal 1984). Overall, badger societies appear protosocial, with some indicators of social structure within allogrooming interactions, but overall it is likely context dependent.

Despotic social style is predicted to be positively related with dominance hierarchy steepness (Balasubramaniam et al. 2012), such that unreciprocated allogrooming should be directed up steeper dominance hierarchies more. Hewitt et al. (2009) studied the steepness of badger dominance hierarchies, based on directed aggression interactions, in the same social-group-years in which we analyzed allogrooming. Surprisingly the two social-group-years in which directed aggression was correlated with unreciprocated allogrooming either did not display a significantly steep direct aggression hierarchy (P 1995), or had the fourth shallowest hierarchy (PO 2004) out of the five social-group-years with a significantly steep hierarchy. This does not support the predicted relationship between greater dominance hierarchy steepness and a greater despotic society (Balasubramaniam et al. 2012)

*Genetic relatedness and allogrooming*

We found no overall significant correlation between either reciprocated or unreciprocated allogrooming and genetic relatedness; thus, allogrooming is not influenced by genetic relatedness. This result might be due to high natal philopatry in badger groups, resulting in a high degree of relatedness and limited variation in relatedness between group members. For example, females and males are related to non-cub group-members by 0.20 [95% confidence interval = 0.16–0.24] and 0.16 [0.13–0.19], respectively (Dugdale et al. 2008).

Evidence for a limited impact of kinship on affiliative relationships has also been found in other species. In both male and female chimpanzees, the majority of affiliative and cooperative dyads were formed between unrelated or distantly related individuals (Langergraber et al. 2007; Langergraber et al. 2009). Among female bonobos, genetic relatedness was not related to the formation of affiliative relationships, defined by grooming and proximity frequencies (Hashimoto et al. 1996). In female Japanese macaques, there was no relationship between relatedness and grooming (Schino et al. 2007). However, dominant captive female bonnet macaques received high rates of unreciprocated allogrooming from kin (Silk 1982). The results from these studies, however, may not be transferable to badgers, as primates live in groups that are a lot more socially structured and intricate than those of the badger. Nevertheless, there are fewer studies on the relationship between genetic relatedness and allogrooming in non-primate species for comparison, and results are mixed, e.g. allogrooming and kinship are positively correlated in cattle (Sato et al. 1993), but not correlated in captive Icelandic horses, *Equus ferus caballus* (de Vries et al. 1994).

## Conclusion

We applied hierarchy analyses in a novel manner to unreciprocated allogrooming behavior, which may provide a useful tool for understanding allogrooming structures in other group-living animals. Our identification of weakly linear and shallow unreciprocated allogrooming hierarchies, and a weak relationship between unreciprocated allogrooming and directed aggression, further supports the weak social structure in badger societies. Indeed, unreciprocated allogrooming may be context dependent, changing with regards to ecological and social contexts throughout the year. It may also relate to an individual’s motives to allogroom, such as their ‘itch’ burden. Overall, we provide a new technique for analyzing allogrooming structures and demonstrate rudimentary indicators of a social structure in allogrooming badgers, reaffirming the protosocial nature of high-density group-living badgers.

## References

Albery GF, Newman C, Ross JB, Macdonald DW, Bansal S, Buesching C. 2020. Negative density-dependent parasitism in a group-living carnivore. Proceedings of the Royal Society B: Biological Sciences. 287(1941):20202655. doi:10.1098/rspb.2020.2655.

Alexander RD. 1974. The evolution of social behavior. Annual Review of Ecology and Systematics. 5:325–383. doi:10.1146/annurev.es.05.110174.001545.

Baker KC, Aureli F. 2000. Coping with conflict during initial encounters in chimpanzees. Ethology. 106(6):527–541. doi:10.1111/j.1439-0310.2000.00553.x.

Balasubramaniam KN, Dittmar K, Berman CM, Butovskaya M, Cooper MA, Majolo B, Ogawa H, Schino G, Thierry B, Waal FBM de. 2012. Hierarchical steepness, counter-aggression, and macaque social style scale. American Journal of Primatology. 74(10):915–925. doi:10.1002/ajp.22044.

Barrett L, Henzi SP. 2006. Monkeys, markets and minds: biological markets and primate sociality. In: Kappeler PM, Schaik CP van, editors. Springer. (Cooperation in Primates and Humans: Mechanisms and Evolution). p. 209–232.

Barrett L, Henzi SP, Weingrill T, Lycett JE, Hill RA. 1999. Market forces predict grooming reciprocity in female baboons. Proceedings of the Royal Society B: Biological Sciences. 266(1420):665–670. doi:10.1098/rspb.1999.0687.

Birkhead TR. 1978. Behavioural adaptations to high density nesting in the common guillemot *Uria aalge*. Animal Behaviour. 26(2):321–331. doi:10.1016/0003-3472(78)90050-7.

Bitetti MSD. 1997. Evidence for an important social role of allogrooming in a platyrrhine primate. Animal Behaviour. 54(1):199–211. doi:10.1006/anbe.1996.0416.

Carne C, Wiper S, Semple S. 2011. Reciprocation and interchange of grooming, agonistic support, feeding tolerance, and aggression in semi-free-ranging Barbary macaques. American Journal of Primatology. 73(11):1127–1133. doi:10.1002/ajp.20979.

Carter G, Leffer L. 2015. Social grooming in bats: are vampire bats exceptional? PloS One. 10(10):e0138430. doi:10.1371/journal.pone.0138430.

Curtis TM, Knowles RJ, Crowell-Davis SL. 2003. Influence of familiarity and relatedness on proximity and allogrooming in domestic cats (*Felis catus*). American Journal of Veterinary Research. 64(9):1151–1154. doi:10.2460/ajvr.2003.64.1151.

Dugdale HL, Ellwood SA, Macdonald DW. 2010. Alloparental behaviour and long-term costs of mothers tolerating other members of the group in a plurally breeding mammal. Animal Behaviour. 80(4):721–735. doi:10.1016/j.anbehav.2010.07.011.

Dugdale HL, Macdonald DW, Pope LC, Burke T. 2007. Polygynandry, extra-group paternity and multiple-paternity litters in European badger (*Meles meles*) social groups. Molecular Ecology. 16(24):5294–5306. doi:10.1111/j.1365-294x.2007.03571.x.

Dugdale HL, Macdonald DW, Pope LC, Johnson PJ, Burke T. 2008. Reproductive skew and relatedness in social groups of European badgers, *Meles meles*. Molecular Ecology. 17(7):1815–1827. doi:10.1111/j.1365-294x.2008.03708.x.

Dunbar R. 1991. Functional significance of social grooming in primates. Folia Primatologica. 57(3):121–131. doi:10.1159/000156574.

Ellwood SA, Newman C, Montgomery RA, Nicosia V, Buesching CD, Markham A, Mascolo C, Trigoni N, Pasztor B, Dyo V, et al. 2017. An active-radio-frequency-identification system capable of identifying co-locations and social-structure: Validation with a wild free-ranging animal. Methods in Ecology and Evolution. 8(12):1822–1831. doi:10.1111/2041-210x.12839.

Forand KJ, Marchinton RL. 1989. Patterns of social grooming in adult white-tailed deer. American Midland Naturalist. 122(2):357. doi:10.2307/2425923.

Freeland WJ. 1976. Pathogens and the evolution of primate sociality. Biotropica. 8(1):12–24. doi: 10.2307/2387816.

Hashimoto C, Takenaka O, Furuichi T. 1996. Matrilineal kin relationship and social behavior of wild bonobos (*Pan paniscus*): Sequencing the D-loop region of mitochondrial DNA. Primates. 37(3):305–318. doi:10.1007/bf02381862.

Henazi SP, Barrett L. 1999. The value of grooming to female primates. Primates. 40(1):47–59. doi:10.1007/bf02557701.

Hewitt S, Macdonald DW, Dugdale HL. 2009. Context-dependent linear dominance hierarchies in social groups of European badgers, *Meles meles*. Animal Behaviour. 77(1):161–169. doi:10.1016/j.anbehav.2008.09.022.

Hutchins M, Barash DP. 1976. Grooming in primates: Implications for its utilitarian function. Primates. 17(2):145–150. doi:10.1007/bf02382848.

Johnson DDP, Stopka P, Macdonald DW. 2004. Ideal flea constraints on group living: unwanted public goods and the emergence of cooperation. Behavioral Ecology. 15(1):181–186. doi:10.1093/beheco/arg093.

Kaburu SSK, Newton-Fisher NE. 2015. Egalitarian despots: hierarchy steepness, reciprocity and the grooming-trade model in wild chimpanzees, *Pan troglodytes*. Animal Behaviour. 99:61–71. doi: 10.1016/j.anbehav.2014.10.018.

Kimura R. 1998. Mutual grooming and preferred associate relationships in a band of free-ranging horses. Applied Animal Behaviour Science. 59(4):265–276. doi:10.1016/s0168-1591(97)00129-9.

Kutsukake N, Clutton-Brock T. 2006. Aggression and submission reflect reproductive conflict between females in cooperatively breeding meerkats *Suricata suricatta*. Behavioral Ecology and Sociobiology. 59(4):541–548. doi:10.1007/s00265-005-0079-7.

Kutsukake N, Clutton-Brock TH. 2006. Social functions of allogrooming in cooperatively breeding meerkats. Animal Behaviour. 72:1059–1068. doi:10.1016/j.anbehav.2006.02.016.

Kutsukake N, Clutton-Brock TH. 2010. Grooming and the value of social relationships in cooperatively breeding meerkats. Animal Behaviour. 79(2):271–279. doi:10.1016/j.anbehav.2009.10.014.

Landau HG. 1951. On dominance relations and the structure of animal societies: I. Effect of inherent characteristics. Bulletin of Mathematical Biophysics. 13(1):1–19.

Langergraber K, Mitani J, Vigilant L. 2009. Kinship and social bonds in female chimpanzees (*Pan troglodytes*). American Journal of Primatology. 71(10):840–851. doi:10.1002/ajp.20711.

Langergraber KE, Mitani JC, Vigilant L. 2007. The limited impact of kinship on cooperation in wild chimpanzees. Proceedings of the National Academy of Sciences. 104(19):7786–7790. doi:10.1073/pnas.0611449104.

Lazaro-Perea C, Arruda M de F, Snowdon CT. 2004. Grooming as a reward? Social function of grooming between females in cooperatively breeding marmosets. Animal Behaviour. 67(4):627–636. doi: 10.1016/j.anbehav.2003.06.004.

Macdonald DW, Newman C. 2002. Population dynamics of badgers (*Meles meles*) in Oxfordshire, UK: numbers, density and cohort life histories, and a possible role of climate change in population growth. Journal of Zoology. 256(1):121–138. doi:10.1017/s0952836902000158.

Macdonald DW, Newman C, Buesching CD, Johnson PJ. 2008. Male-biased movement in a high-density population of the Eurasian badger (*Meles meles*). Journal of Mammalogy. 89(5):10777–11086. doi:10.1644/07-mamm-a-185.1.

Macdonald DW, Stewart PD, Stopka P, Yamaguchi N. 2000. Measuring the dynamics of mammalian societies: an ecologist's guide to ethological methods. In: Boitani L, Fuller TK, editors. Columbia University Press. (Research Techniques in Animal Ecology: Controversies and Consequences). p. 332–388.

McLaren GW, Thornton PD, Newman C, Buesching CD, Baker SE, Mathews F, Macdonald DW. 2005. The use and assessment of ketamine-medetomidine-butorphanol combinations for field anaesthesia in wild European badgers (*Meles meles*). Veterinary Anaesthesia and Analgesia. 32(6):367–372. doi:10.1111/j.1467-2995.2005.00206.x.

Mehlman PT, Chapais B. 1988. Differential effects of kinship, dominance, and the mating season on female allogrooming in a captive group of *Macaca fuscata*. Primates. 29(2):195–217.

Miyazawa E, Seguchi A, Takahashi N, Motai A, Izawa E. 2020. Different patterns of allopreening in the same-sex and opposite-sex interactions of juvenile large-billed crows (*Corvus macrorhynchos*). Ethology. 126(2):195–206. doi:10.1111/eth.12992. https://doi.org/10.1111/eth.12992.

Mooring MS, Hart BL. 1993. Effects of relatedness, dominance, age, and association on reciprocal allogrooming by captive impala. Ethology. 94(3):207–220. doi:10.1111/j.1439-0310.1993.tb00561.x.

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):1–11.

Noë R, Hammerstein P. 1995. Biological markets. Trends in Ecology & Evolution. 10(8):336–339. doi: 10.1016/S0169-5347(00)89123-5.

O’Brien TG. 1993. Allogrooming behaviour among adult female wedge-capped capuchin monkeys. Animal Behaviour. 46(3):499–510. doi:10.1006/anbe.1993.1218.

Parr LA, Matheson MD, Bernstein IS, Waal FBM de. 1997. Grooming down the hierarchy: allogrooming in captive brown capuchin monkeys, *Cebus apella*. Animal Behaviour. 54(2):361–367. doi:10.1006/anbe.1996.0419.

Queller DC, Goodnight KF. 1989. Estimating relatedness using genetic markers. Evolution. 43(2):258–275. doi: 10.1111/j.1558-5646.1989.tb04226.x.

R Core Team R. 2017. R: A language and environment for statistical computing. https://www.R-project.org.

Radford AN, Plessis MA du. 2006. Dual function of allopreening in the cooperatively breeding green woodhoopoe, *Phoeniculus purpureus*. Behavioral Ecology and Sociobiology. 61(2):221–230.

Riek RF. 1962. Studies on the reactions of animals to infestation with ticks. VI. Resistance of cattle to infestation with the tick *Boophilus microplus* (Canestrini). Australian Journal of Agricultural Research. 13(3):532–550. doi:10.1071/ar9620532.

Sade DS. 1965. Some aspects of parent-offspring and sibling relations in a group of rhesus monkeys, with a discussion of grooming. American Journal of Physical Anthropology. 23(1):1–17. doi:10.1002/ajpa.1330230115.

Sanchez-Tojar A, Schroeder J, Farine DR. 2017. A practical guide for inferring reliable dominance hierarchies and estimating their uncertainty. Morand-Ferron J, editor. Journal of Animal Ecology. 87(3):594–608. doi:10.1111/1365-2656.12776.

Šárová R, Gutmann AK, Špinka M, Stěhulová I, Winckler C. 2016. Important role of dominance in allogrooming behaviour in beef cattle. Applied Animal Behaviour Science. 181:41–48.

Sato S, Tarumizu K, Hatae K. 1993. The influence of social factors on allogrooming in cows. Applied Animal Behaviour Science. 38(3–4):235–244. doi:10.1016/0168-1591(93)90022-h.

Schino G, Maestripieri D, Scucchi S, Turillazzi PG. 1990. Social tension in familiar and unfamiliar pairs of long-tailed macaques. Behaviour. 113(3):264–272. doi:https://doi.org/10.1163/156853990X00518.

Schino G, Sorrentino EP di, Tiddi B. 2007. Grooming and coalitions in Japanese macaques (*Macaca fuscata*): Partner choice and the time frame reciprocation. Journal of Comparative Psychology. 121(2):181–188. doi:10.1037/0735-7036.121.2.181.

Schmid VS, Vries H de. 2013. Finding a dominance order most consistent with a linear hierarchy: an improved algorithm for the I&SI method. Animal Behaviour. 86(5):1097–1105. doi: 10.1016/j.anbehav.2013.08.019.

Schweinfurth MK, Stieger B, Taborsky M. 2017. Experimental evidence for reciprocity in allogrooming among wild-type Norway rats. Scientific Reports. 7(1):4010. doi:10.1038/s41598-017-03841-3.

Seyfarth RM. 1977. A model of social grooming among adult female monkeys. Journal of Theoretical Biology. 65(4):671–698. doi:10.1016/0022-5193(77)90015-7.

Seyfarth RM, Cheney DL. 1984. Grooming, alliances and reciprocal altruism in vervet monkeys. Nature. 308(5959):541–543. doi:10.1038/308541a0.

Silk JB. 1982. Altruism among female *Macaca radiata*: Explanations and analysis of patterns of grooming and coalition formation. Behaviour. 79(2):162–188. doi:10.1163/156853982x00238.

Silva J da, Macdonald DW, Evans PGH. 1994. Net costs of group living in a solitary forager, the Eurasian badger (*Meles meles*). Behavioral Ecology. 5(2):151–158. doi:10.1093/beheco/5.2.151.

Singh Mridula, Krishna BA, Singh Mewa. 2006. Dominance hierarchy and social grooming in female lion-tailed macaques (*Macaca silenus*) in the Western Ghats, India. Journal of Biosciences. 31(3):369–377. doi:10.1007/bf02704110.

Sokal RR, Rohlf FJ. 1994. Biometry: Principles and Practice of Statistics in Biological Research. 3rd ed. W.H. Freeman (W.H. Freeman).

Sparks J. 1967. Allogrooming in primates: A review. Aldine Transaction. (Primate Ethology.). p. 148–175. http://www.worldcat.org/title/primate-ethology/oclc/994145336.

Stammbach E, Kummer H. 1982. Individual contributions to a dyadic interaction: An analysis of baboon grooming. Animal Behaviour. 30(4):964–971. doi:10.1016/s0003-3472(82)80184-x.

Stewart PD, Ellwood SA, Macdonald DW. 1997. Remote video-surveillance of wildlife - an introduction from experience with the European badger *Meles meles*. Mammal Review. 27(4):185–204. doi: 10.1111/j.1365-2907.1997.tb00448.x.

Stewart PD, Macdonald DW. 1997. Age, sex, and condition as predictors of moult and the efficacy of a novel fur-clip technique for individual marking of the European badger (*Meles meles*). Journal of Zoology. 241(3):543–550. doi:10.1111/j.1469-7998.1997.tb04846.x.

Stewart PD, Macdonald DW. 2003. Badgers and badger fleas: strategies and counter-strategies. Ethology. 109(9):751–764. doi: 10.1046/j.1439-0310.2003.00910.x.

Tiddi B, Aureli F, Schino G. 2012. Grooming up the hierarchy: The exchange of grooming and rank-related benefits in a New World primate. PLoS ONE. 7(5):e36641. doi:10.1371/journal.pone.0036641.

Vries H de. 1995. An improved test of linearity in dominance hierarchies containing unknown or tied relationships. Animal Behaviour. 50:1375–1389. doi:10.1016/0003-3472(95)80053-0.

Vries H de. 1998. Finding a dominance order most consistent with a linear hierarchy: a new procedure and review. Animal Behaviour. 55:827–843. doi:10.1006/anbe.1997.0708.

Vries H de, Netto WJ, Hanegraaf PLH. 1993. MatMan: a program for the analysis of sociometric matrices and behavioural transition matrices. Behaviour. 125(3):157–175. doi:10.1163/156853993x00218.

Vries H de, Stevens JMG, Vervaecke H. 2006. Measuring and testing the steepness of dominance hierarchies. Animal Behaviour. 71(3):585–592. doi:10.1016/j.anbehav.2005.05.015.

Vries HD, Dierendonck MCV, Schilder MBH. 1994. An Analysis of Dominance, Its Behavioural Parameters and Possible Determinants in a Herd of Icelandic Horses in Captivity. Neth J Zool. 45(3–4):362–385. doi:10.1163/156854295x00366.

Waal FBM de. 1984. Coping with social tension: Sex differences in the effect of food provision to small rhesus monkey groups. Animal Behaviour. 32(3):765–773. doi: 10.1016/S0003-3472(84)80152-9.

Walsh PS, Metzger DA, Higuchi R. 1991. Chelex 100 as a medium for simple extraction of DNA for PCR-based typing from forensic material. BioTechniques. 10(4):506–513.

Willadsen P. 1980. Immunity to ticks. Advances in Parasitology. 18:293. doi: 10.1016/S0065-308X(08)60402-9.

Woodroffe R, Macdonald DW. 1993. Badger sociality - models of spatial grouping. Symposia of the Zoological Society of London. 65:145–169.

**Table 1:** Social-group-year compositions by sex, excluding cubs, which were not included in any analyses.

| | **1995** | | **2004** | | **2005** | |
|---|---|---|---|---|---|---|
| | **SH** | **P** | **P** | **PO** | **P** | **PO** |
| Females | 4 | 7 | 4 | 4 | 7 | 4* |
| Males | 10 | 4 | 3 | 3 | 2 | 2 |
| Total number of individuals | 14 | 11 | 7 | 7 | 9 | 6 |
| Sex ratio (proportion of females) | 0.29 | 0.64 | 0.57 | 0.57 | 0.78 | 0.67 |

* One badger was excluded from all analyses as it led to structural zeros (i.e. they were not observed with at least one other individual and so there was at least one dyad where allogrooming could not be measured)

**Table 2:** Linearity and steepness of unreciprocated allogrooming hierarchies for all six social-group-years, with significant results in bold. The *h* value represents the unbiased estimate of Landau's (1951) linearity index (de Vries 1995). Improved linearity test (de Vries 1995) right-tailed *P* values < 0.05 indicate a significantly linear hierarchy, whereas, left-tailed *P* < 0.05 indicate a significantly non-linear hierarchy.

| | **1995** | | **2004** | | **2005** | |
|---|---|---|---|---|---|---|
| | **SH** | **P** | **P** | **PO** | **P** | **PO** |
| Number of individuals | 14 | 11 | 7 | 7 | 9 | 5 |
| Number of pairs | 91 | 55 | 21 | 21 | 36 | 10 |
| Unreciprocated allogrooming events (weighted by number of bouts) | 360 | 189 | 259 | 230 | 852 | 167 |
| Linearity index ($h_o$) | 0.248 | 0.275 | 0.571 | 0.784 | 0.700 | 0.950 |
| $P_{right}$ | 0.303 | 0.428 | 0.194 | 0.067 | **0.006** | 0.121 |
| $P_{left}$ | 0.697 | 0.572 | 0.806 | 0.961 | 0.994 | 0.879 |
| Steepness of hierarchy | 0.209 | 0.143 | 0.302 | 0.379 | 0.488 | 0.529 |
| $P_{right}$ | **0.001** | **<0.001** | 0.284 | **0.034** | **0.002** | 0.105 |

**Table 3** Kendall’s row-wise correlation results, testing whether individuals show: 1) Higher levels of unreciprocated grooming towards individuals that direct more aggression at them; 2) Lower levels of unreciprocated grooming towards more related individuals; 3) Higher levels of reciprocated grooming towards more related individuals; and, 4) Higher levels of unreciprocated grooming towards individuals that reciprocate allogrooming more. N = number of badgers. *P*-values in bold are significant at $P < 0.05$.

|  | Year | 1995 |  | 2004 |  | 2005 |  |
|---|---|---|---|---|---|---|---|
|  | Social-group | SH | P | P | PO | P | PO |
| Unreciprocated allogrooming and directed aggression | Kr | 65^ | 28^ | -22 | 27 | 0 | 12 |
|  | N | 14 | 11 | 7 | 7 | 9 | 5 |
|  | P-right | 0.109 | 0.051 | 0.926 | **0.045** | 0.514 | 0.075 |
| Unreciprocated allogrooming and relatedness | Kr | 17 | 11 | 21 | 8 | -20 | 9 |
|  | N | 14 | 10* | 7 | 7 | 9 | 5 |
|  | P-left | 0.613 | 0.686 | 0.906 | 0.745 | 0.215 | 0.867 |
| Reciprocated allogrooming and relatedness | Kr | 25 | -1 | 13 | 0 | 17 | 3 |
|  | N | 14 | 10* | 7 | 7 | 9 | 5 |
|  | P-right | 0.367 | 0.517 | 0.202 | 0.521 | 0.246 | 0.400 |

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| Unreciprocated allogrooming and reciprocated allogrooming | Kr | 124 | 54 | 56 | 38 | 106 | 20 |
| | N | 14 | 11 | 7 | 7 | 9 | 5 |
| | P-right | **0.020** | **0.008** | **<0.001** | **0.003** | **<0.001** | **0.008** |

* One badger was not genotyped

^ Results differ from Hewitt *et al*. (2009), as they excluded two badgers from P 1995 due to structural zeros in their hierarchy analysis, which we have included in our row-wise correlation, and re-analysis of SH 1995 led to the inclusion of three more unreciprocated allogrooming events

# **Supplementary materials for** “Unreciprocated allogrooming hierarchies in a population of wild group-living mammals”

**Figure S1:** Matrices of the number of observed dyadic unreciprocated allogrooming events for each social-group-year, and the sex of each badger. Rows represent individuals who received unreciprocated allogrooming (winners) and columns represent individuals who initiated unreciprocated allogrooming events (losers). The number of unreciprocated allogrooming events were weighted by the number of bouts when dyads were recorded on camera, then multiplied by 100 and rounded to whole numbers.

**SH 1995**

| | **M** | **M** | **M** | **M** | **M** | **F** | **M** | **M** | **M** | **F** | **F** | **M** | **F** | **M** |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **M** | * | 0 | 0 | 7 | 13 | 0 | 0 | 0 | 0 | 0 | 0 | 9 | 0 | 0 |
| **M** | 0 | * | 0 | 3 | 4 | 0 | 3 | 2 | 0 | 0 | 0 | 2 | 0 | 0 |
| **M** | 0 | 0 | * | 3 | 0 | 4 | 0 | 0 | 0 | 0 | 0 | 0 | 4 | 3 |
| **M** | 0 | 5 | 0 | * | 2 | 0 | 0 | 1 | 0 | 0 | 2 | 6 | 7 | 0 |
| **M** | 13 | 4 | 0 | 2 | * | 3 | 3 | 3 | 0 | 0 | 0 | 3 | 6 | 8 |
| **F** | 0 | 4 | 0 | 3 | 3 | * | 0 | 6 | 5 | 0 | 0 | 3 | 6 | 0 |
| **M** | 0 | 3 | 0 | 4 | 3 | 0 | * | 14 | 4 | 0 | 0 | 10 | 6 | 6 |
| **M** | 0 | 5 | 0 | 4 | 6 | 6 | 0 | * | 0 | 0 | 0 | 2 | 0 | 2 |
| **M** | 0 | 0 | 0 | 22 | 8 | 0 | 0 | 5 | * | 0 | 0 | 0 | 0 | 5 |
| **F** | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | * | 0 | 0 | 0 | 0 |
| **F** | 0 | 0 | 0 | 2 | 0 | 3 | 5 | 2 | 0 | 0 | * | 3 | 0 | 0 |
| **M** | 0 | 3 | 0 | 10 | 0 | 3 | 2 | 2 | 0 | 0 | 3 | * | 3 | 3 |
| **F** | 0 | 4 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 6 | * | 0 |
| **M** | 0 | 6 | 3 | 7 | 3 | 0 | 0 | 0 | 5 | 0 | 0 | 3 | 9 | * |

**P 1995**

| | **F** | **F** | **M** | **F** | **F** | **M** | **M** | **F** | **F** | **F** | **M** |
|---|---|---|---|---|---|---|---|---|---|---|---|

| | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| **F** | * | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 0 |
| **F** | 0 | * | 0 | 0 | 0 | 0 | 17 | 0 | 7 | 0 | 0 |
| **M** | 11 | 0 | * | 0 | 0 | 6 | 0 | 0 | 0 | 0 | 0 |
| **F** | 0 | 0 | 0 | * | 0 | 0 | 4 | 0 | 0 | 0 | 0 |
| **F** | 0 | 0 | 14 | 20 | * | 25 | 0 | 10 | 0 | 0 | 0 |
| **M** | 3 | 0 | 1 | 0 | 0 | * | 0 | 0 | 0 | 0 | 0 |
| **M** | 0 | 0 | 0 | 4 | 0 | 0 | * | 0 | 0 | 8 | 3 |
| **F** | 30 | 0 | 0 | 0 | 10 | 0 | 0 | * | 4 | 0 | 0 |
| **F** | 0 | 0 | 0 | 0 | 0 | 7 | 0 | 0 | * | 10 | 0 |
| **F** | 8 | 0 | 0 | 6 | 0 | 14 | 0 | 0 | 0 | * | 0 |
| **M** | 0 | 0 | 0 | 0 | 0 | 0 | 14 | 0 | 0 | 0 | * |

**P 2004**

| | **F** | **M** | **M** | **F** | **F** | **F** | **M** |
|---|---|---|---|---|---|---|---|
| **F** | * | 10 | 2 | 20 | 24 | 3 | 6 |
| **M** | 1 | * | 4 | 4 | 9 | 3 | 0 |
| **M** | 3 | 16 | * | 29 | 9 | 5 | 0 |
| **F** | 2 | 4 | 6 | * | 3 | 2 | 0 |
| **F** | 13 | 6 | 5 | 8 | * | 7 | 0 |
| **F** | 4 | 3 | 3 | 4 | 11 | * | 7 |
| **M** | 3 | 0 | 0 | 0 | 0 | 20 | * |

**PO 2004**

| | **M** | **F** | **F** | **M** | **F** | **F** | **M** |
|---|---|---|---|---|---|---|---|
| **M** | * | 0 | 0 | 5 | 11 | 0 | 15 |
| **F** | 2 | * | 11 | 9 | 9 | 0 | 12 |
| **F** | 3 | 3 | * | 7 | 10 | 25 | 23 |
| **M** | 3 | 4 | 0 | * | 5 | 0 | 15 |
| **F** | 1 | 2 | 2 | 10 | * | 0 | 8 |
| **F** | 0 | 0 | 0 | 0 | 0 | * | 0 |
| **M** | 4 | 0 | 15 | 10 | 6 | 0 | * |

**P 2005**

| | F | M | F | F | M | F | F | F | F |
|---|---|---|---|---|---|---|---|---|---|
| **F** | * | 17 | 3 | 16 | 22 | 17 | 8 | 10 | 55 |
| **M** | 1 | * | 6 | 7 | 22 | 5 | 4 | 3 | 22 |
| **F** | 0 | 0 | * | 2 | 3 | 0 | 5 | 0 | 10 |
| **F** | 4 | 8 | 12 | * | 5 | 9 | 6 | 5 | 42 |
| **M** | 5 | 4 | 0 | 5 | * | 6 | 2 | 11 | 23 |
| **F** | 7 | 12 | 4 | 1 | 8 | * | 2 | 8 | 0 |
| **F** | 3 | 4 | 14 | 6 | 2 | 7 | * | 17 | 0 |
| **F** | 4 | 50 | 120 | 7 | 20 | 32 | 22 | * | 59 |
| **F** | 0 | 11 | 10 | 0 | 23 | 0 | 8 | 6 | * |

**PO 2005**

| | M | F | F | M | F |
|---|---|---|---|---|---|
| **M** | * | 0 | 6 | 11 | 6 |
| **F** | 11 | * | 3 | 20 | 35 |
| **F** | 9 | 3 | * | 16 | 11 |
| **M** | 3 | 7 | 4 | * | 8 |
| **F** | 2 | 0 | 9 | 3 | * |

10

**Figure S2:** Matrices of the number of dyadic acts of directed aggression for each social-group-year. Rows represent individuals that initiated directed aggression (winners) and columns show individuals who received directed aggression (losers). The number of directed aggression events were weighted by the number of bouts for which dyads were recorded on camera, then multiplied by 100 and rounded to whole numbers.

**SH 1995**

| | **M** | **M** | **M** | **M** | **M** | **F** | **M** | **M** | **M** | **F** | **F** | **M** | **F** | **M** |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **M** | * | 0 | 0 | 7 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 18 | 0 | 0 |
| **M** | 0 | * | 4 | 7 | 7 | 0 | 0 | 3 | 5 | 0 | 0 | 3 | 4 | 0 |
| **M** | 0 | 4 | * | 0 | 4 | 0 | 0 | 8 | 0 | 0 | 0 | 6 | 0 | 0 |
| **M** | 0 | 0 | 3 | * | 2 | 0 | 0 | 0 | 0 | 0 | 2 | 1 | 0 | 6 |
| **M** | 0 | 0 | 0 | 2 | * | 0 | 0 | 0 | 4 | 0 | 0 | 0 | 0 | 3 |
| **F** | 33 | 0 | 0 | 11 | 17 | * | 0 | 10 | 0 | 0 | 0 | 21 | 0 | 10 |
| **M** | 0 | 0 | 0 | 0 | 0 | 0 | * | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| **M** | 0 | 2 | 0 | 7 | 3 | 0 | 4 | * | 0 | 0 | 0 | 8 | 0 | 2 |
| **M** | 0 | 5 | 0 | 2 | 0 | 0 | 0 | 0 | * | 0 | 0 | 3 | 0 | 0 |
| **F** | 0 | 0 | 8 | 5 | 29 | 0 | 0 | 8 | 25 | * | 0 | 0 | 11 | 8 |
| **F** | 14 | 3 | 9 | 8 | 0 | 3 | 5 | 5 | 0 | 0 | * | 0 | 14 | 13 |
| **M** | 0 | 3 | 0 | 4 | 0 | 0 | 0 | 2 | 9 | 0 | 0 | * | 0 | 3 |
| **F** | 0 | 4 | 0 | 3 | 3 | 0 | 0 | 0 | 5 | 0 | 0 | 0 | * | 0 |
| **M** | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 3 | 0 | * |

**P 1995**

| | **F** | **F** | **M** | **F** | **F** | **M** | **M** | **F** | **F** | **F** | **M** |
|---|---|---|---|---|---|---|---|---|---|---|---|
| **F** | * | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| **F** | 0 | * | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 17 |
| **M** | 0 | 0 | * | 0 | 0 | 3 | 0 | 0 | 8 | 0 | 0 |
| **F** | 0 | 0 | 0 | * | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| **F** | 0 | 0 | 14 | 0 | * | 0 | 17 | 0 | 0 | 0 | 0 |
| **M** | 0 | 20 | 0 | 0 | 0 | * | 0 | 0 | 0 | 0 | 0 |

|  |  |  |  |  |  |  |  |  |  |  |  |
|---|---|---|---|---|---|---|---|---|---|---|---|
| **M** | 0 | 0 | 0 | 10 | 0 | 0 | * | 0 | 13 | 0 | 4 |
| **F** | 0 | 0 | 0 | 0 | 10 | 0 | 0 | * | 0 | 0 | 20 |
| **F** | 0 | 0 | 0 | 0 | 0 | 7 | 13 | 0 | * | 10 | 0 |
| **F** | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | * | 18 |
| **M** | 0 | 0 | 0 | 6 | 0 | 0 | 4 | 0 | 0 | 0 | * |

**P 2004**

|  | **F** | **M** | **M** | **F** | **F** | **F** | **M** |
|---|---|---|---|---|---|---|---|
| **F** | * | 5 | 9 | 2 | 2 | 2 | 6 |
| **M** | 4 | * | 32 | 4 | 3 | 2 | 7 |
| **M** | 5 | 4 | * | 0 | 2 | 0 | 7 |
| **F** | 12 | 13 | 13 | * | 5 | 0 | 14 |
| **F** | 5 | 3 | 15 | 3 | * | 7 | 13 |
| **F** | 9 | 17 | 14 | 14 | 22 | * | 13 |
| **M** | 0 | 0 | 7 | 0 | 0 | 0 | * |

**PO 2004**

|  | **M** | **F** | **F** | **M** | **F** | **F** | **M** |
|---|---|---|---|---|---|---|---|
| **M** | * | 0 | 7 | 12 | 7 | 0 | 46 |
| **F** | 14 | * | 11 | 11 | 9 | 0 | 32 |
| **F** | 4 | 0 | * | 10 | 3 | 0 | 18 |
| **M** | 2 | 0 | 0 | * | 2 | 0 | 17 |
| **F** | 4 | 0 | 2 | 3 | * | 0 | 2 |
| **F** | 0 | 0 | 0 | 0 | 0 | * | 0 |
| **M** | 8 | 0 | 3 | 8 | 6 | 33 | * |

**P 2005**

|  | **F** | **M** | **F** | **F** | **M** | **F** | **F** | **F** | **F** |
|---|---|---|---|---|---|---|---|---|---|
| **F** | * | 7 | 10 | 5 | 41 | 25 | 44 | 0 | 9 |
| **M** | 1 | * | 0 | 0 | 6 | 2 | 0 | 0 | 0 |
| **F** | 3 | 0 | * | 2 | 8 | 0 | 10 | 0 | 0 |

| | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| **F** | 6 | 8 | 0 | * | 7 | 13 | 31 | 4 | 0 |
| **M** | 0 | 10 | 0 | 0 | * | 4 | 5 | 2 | 0 |
| **F** | 0 | 0 | 0 | 0 | 6 | * | 3 | 0 | 0 |
| **F** | 0 | 0 | 0 | 0 | 2 | 2 | * | 0 | 0 |
| **F** | 1 | 13 | 0 | 0 | 15 | 4 | 6 | * | 0 |
| **F** | 0 | 0 | 0 | 0 | 3 | 17 | 8 | 0 | * |

**PO 2005**

| | **M** | **F** | **F** | **M** | **F** |
|---|---|---|---|---|---|
| **M** | * | 0 | 2 | 13 | 6 |
| **F** | 3 | * | 0 | 9 | 20 |
| **F** | 2 | 0 | * | 0 | 11 |
| **M** | 2 | 0 | 2 | * | 3 |
| **F** | 2 | 0 | 0 | 0 | * |

16

**Figure S3:** Matrices of the Queller and Goodnight relatedness (*R*) between individuals for each social-group-year. *R* values of 0 are completely unrelated individuals, and *R* values of 1 are identical individuals.

**SH 1995**

| | **M** | **M** | **M** | **M** | **M** | **F** | **M** | **M** | **M** | **F** | **F** | **M** | **F** | **M** |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **M** | * | 0.523 | 0.727 | 0.302 | 0.397 | 0.541 | 0.639 | 0.389 | 0.383 | 0.324 | 0.526 | 0.340 | 0.558 | 0.571 |
| **M** | 0.523 | * | 0.570 | 0.616 | 0.547 | 0.387 | 0.774 | 0.638 | 0.691 | 0.750 | 0.598 | 0.685 | 0.742 | 0.648 |
| **M** | 0.727 | 0.570 | * | 0.395 | 0.296 | 0.624 | 0.646 | 0.469 | 0.393 | 0.334 | 0.605 | 0.317 | 0.456 | 0.502 |
| **M** | 0.302 | 0.616 | 0.395 | * | 0.337 | 0.641 | 0.530 | 0.602 | 0.297 | 0.469 | 0.584 | 0.612 | 0.488 | 0.456 |
| **M** | 0.397 | 0.547 | 0.296 | 0.337 | * | 0.017 | 0.702 | 0.632 | 0.633 | 0.694 | 0.164 | 0.577 | 0.473 | 0.258 |
| **F** | 0.541 | 0.387 | 0.624 | 0.641 | 0.017 | * | 0.350 | 0.334 | 0.181 | 0.311 | 0.647 | 0.419 | 0.430 | 0.398 |
| **M** | 0.639 | 0.774 | 0.646 | 0.530 | 0.702 | 0.350 | * | 0.726 | 0.694 | 0.641 | 0.548 | 0.652 | 0.626 | 0.601 |
| **M** | 0.389 | 0.638 | 0.469 | 0.602 | 0.632 | 0.334 | 0.726 | * | 0.632 | 0.706 | 0.632 | 0.796 | 0.528 | 0.501 |
| **M** | 0.383 | 0.691 | 0.393 | 0.297 | 0.633 | 0.181 | 0.694 | 0.632 | * | 0.688 | 0.466 | 0.508 | 0.605 | 0.507 |
| **F** | 0.324 | 0.750 | 0.334 | 0.469 | 0.694 | 0.311 | 0.641 | 0.706 | 0.688 | * | 0.439 | 0.827 | 0.700 | 0.474 |
| **F** | 0.526 | 0.598 | 0.605 | 0.584 | 0.164 | 0.647 | 0.548 | 0.632 | 0.466 | 0.439 | * | 0.499 | 0.557 | 0.712 |
| **M** | 0.340 | 0.685 | 0.317 | 0.612 | 0.577 | 0.419 | 0.652 | 0.796 | 0.508 | 0.827 | 0.499 | * | 0.614 | 0.410 |
| **F** | 0.558 | 0.742 | 0.456 | 0.488 | 0.473 | 0.430 | 0.626 | 0.528 | 0.605 | 0.700 | 0.557 | 0.614 | * | 0.492 |
| **M** | 0.571 | 0.648 | 0.502 | 0.456 | 0.258 | 0.398 | 0.601 | 0.501 | 0.507 | 0.474 | 0.712 | 0.410 | 0.492 | * |

**P**
**1995**

| | F | F | M | F | F | M | M | F | F | F |
|---|---|---|---|---|---|---|---|---|---|---|
| **F** | * | 0.329 | 0.146 | 0.229 | 0.508 | 0.276 | -0.043 | 0.251 | 0.085 | 0.226 |
| **F** | 0.329 | * | 0.703 | 0.579 | 0.548 | 0.717 | -0.144 | 0.108 | 0.231 | 0.168 |
| **M** | 0.146 | 0.703 | * | 0.684 | 0.451 | 0.648 | -0.109 | 0.232 | 0.403 | -0.093 |
| **F** | 0.229 | 0.579 | 0.684 | * | 0.559 | 0.468 | -0.230 | 0.191 | 0.466 | -0.097 |
| **F** | 0.508 | 0.548 | 0.451 | 0.559 | * | 0.311 | -0.399 | -0.093 | 0.004 | 0.038 |
| **M** | 0.276 | 0.717 | 0.648 | 0.468 | 0.311 | * | -0.280 | 0.365 | 0.487 | 0.043 |
| **M** | -0.043 | -0.144 | -0.109 | -0.230 | -0.399 | -0.280 | * | 0.156 | -0.130 | 0.269 |
| **F** | 0.251 | 0.108 | 0.232 | 0.191 | -0.093 | 0.365 | 0.156 | * | 0.665 | 0.093 |
| **F** | 0.085 | 0.231 | 0.403 | 0.466 | 0.004 | 0.487 | -0.130 | 0.665 | * | -0.184 |
| **F** | 0.226 | 0.168 | -0.093 | -0.097 | 0.038 | 0.043 | 0.269 | 0.093 | -0.184 | * |

**P**
**2004**

| | F | M | M | F | F | F | M |
|---|---|---|---|---|---|---|---|
| **F** | * | 0.230 | 0.423 | 0.312 | 0.813 | 0.393 | -0.029 |
| **M** | 0.230 | * | 0.067 | 0.292 | 0.465 | 0.118 | 0.448 |
| **M** | 0.423 | 0.067 | * | 0.408 | 0.356 | 0.125 | 0.105 |
| **F** | 0.312 | 0.292 | 0.408 | * | 0.238 | 0.326 | 0.104 |

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| **F** | 0.813 | 0.465 | 0.356 | 0.238 | * | 0.371 | 0.100 |
| **F** | 0.393 | 0.118 | 0.125 | 0.326 | 0.371 | * | 0.297 |
| **M** | -0.029 | 0.448 | 0.105 | 0.104 | 0.100 | 0.297 | * |

**PO 2004**

| | **M** | **F** | **F** | **M** | **F** | **F** | **M** |
|---|---|---|---|---|---|---|---|
| **M** | * | 0.257 | 0.215 | 0.543 | 0.554 | -0.038 | 0.315 |
| **F** | 0.257 | * | 0.371 | 0.406 | 0.280 | 0.466 | 0.616 |
| **F** | 0.215 | 0.371 | * | 0.383 | 0.239 | 0.208 | 0.386 |
| **M** | 0.543 | 0.406 | 0.383 | * | 0.275 | 0.006 | 0.342 |
| **F** | 0.554 | 0.280 | 0.239 | 0.275 | * | 0.067 | 0.173 |
| **F** | -0.038 | 0.466 | 0.208 | 0.006 | 0.067 | * | 0.558 |
| **M** | 0.315 | 0.616 | 0.386 | 0.342 | 0.173 | 0.558 | * |

**P 2005**

| | **F** | **M** | **F** | **F** | **M** | **F** | **F** | **F** | **F** |
|---|---|---|---|---|---|---|---|---|---|
| **F** | * | 0.523 | 0.481 | 0.275 | 0.173 | 0.128 | 0.018 | 0.360 | 0.376 |
| **M** | 0.523 | * | 0.408 | 0.125 | 0.063 | 0.203 | 0.008 | 0.423 | 0.356 |
| **F** | 0.481 | 0.408 | * | 0.326 | 0.213 | 0.494 | 0.302 | 0.312 | 0.238 |
| **F** | 0.275 | 0.125 | 0.326 | * | 0.607 | 0.119 | 0.103 | 0.393 | 0.371 |

| | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| **M** | 0.173 | 0.063 | 0.213 | 0.607 | * | 0.402 | 0.390 | 0.224 | 0.194 |
| **F** | 0.128 | 0.203 | 0.494 | 0.119 | 0.402 | * | 0.522 | -0.024 | -0.019 |
| **F** | 0.018 | 0.008 | 0.302 | 0.103 | 0.390 | 0.522 | * | 0.127 | 0.050 |
| **F** | 0.360 | 0.423 | 0.312 | 0.393 | 0.224 | -0.024 | 0.127 | * | 0.813 |
| **F** | 0.376 | 0.356 | 0.238 | 0.371 | 0.194 | -0.019 | 0.050 | 0.813 | * |

**PO 2005**

| | **M** | **F** | **F** | **M** | **F** |
|---|---|---|---|---|---|
| **M** | * | 0.257 | 0.215 | 0.315 | 0.225 |
| **F** | 0.257 | * | 0.371 | 0.616 | 0.728 |
| **F** | 0.215 | 0.371 | * | 0.386 | 0.419 |
| **M** | 0.315 | 0.616 | 0.386 | * | 0.429 |
| **F** | 0.225 | 0.728 | 0.419 | 0.429 | * |

**Figure S4:** Matrices of the number of observed dyadic reciprocated allogrooming events for each social-group-year. Rows represent individuals who received reciprocated allogrooming and columns represent individuals who initiated reciprocated allogrooming events.

**SH 1995**

| | M | M | M | M | M | F | M | M | M | F | F | M | F | M |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **M** | * | 33 | 0 | 14 | 50 | 17 | 0 | 20 | 0 | 0 | 0 | 18 | 0 | 20 |
| **M** | 0 | * | 7 | 19 | 4 | 4 | 3 | 13 | 0 | 0 | 10 | 32 | 4 | 0 |
| **M** | 0 | 4 | * | 15 | 7 | 7 | 9 | 18 | 13 | 23 | 14 | 13 | 8 | 19 |
| **M** | 7 | 22 | 13 | * | 4 | 5 | 0 | 12 | 5 | 10 | 4 | 14 | 3 | 7 |
| **M** | 0 | 11 | 0 | 6 | * | 0 | 3 | 14 | 8 | 0 | 11 | 8 | 21 | 0 |
| **F** | 17 | 11 | 4 | 0 | 7 | * | 4 | 3 | 0 | 27 | 8 | 5 | 0 | 13 |
| **M** | 0 | 3 | 9 | 7 | 3 | 4 | * | 39 | 4 | 0 | 5 | 12 | 0 | 16 |
| **M** | 0 | 15 | 3 | 7 | 3 | 3 | 18 | * | 5 | 8 | 2 | 8 | 0 | 17 |
| **M** | 0 | 0 | 0 | 15 | 12 | 0 | 8 | 5 | * | 0 | 4 | 3 | 11 | 14 |
| **F** | 0 | 0 | 0 | 15 | 0 | 0 | 0 | 8 | 0 | * | 0 | 0 | 22 | 8 |
| **F** | 0 | 8 | 5 | 6 | 5 | 0 | 5 | 18 | 0 | 4 | * | 0 | 5 | 0 |
| **M** | 18 | 28 | 0 | 13 | 3 | 3 | 5 | 8 | 9 | 0 | 0 | * | 3 | 11 |
| **F** | 0 | 11 | 4 | 17 | 3 | 0 | 0 | 4 | 5 | 0 | 5 | 7 | * | 6 |
| **M** | 0 | 0 | 7 | 4 | 3 | 8 | 0 | 6 | 5 | 8 | 3 | 19 | 15 | * |

**P 1995**

| | F | F | M | F | F | M | M | F | F | F | M |
|---|---|---|---|---|---|---|---|---|---|---|---|
| **F** | * | 0 | 3 | 0 | 0 | 6 | 18 | 0 | 11 | 0 | 18 |
| **F** | 0 | * | 0 | 20 | 20 | 20 | 0 | 11 | 0 | 0 | 0 |
| **M** | 3 | 0 | * | 0 | 0 | 14 | 0 | 0 | 0 | 0 | 0 |
| **F** | 15 | 0 | 0 | * | 0 | 0 | 15 | 0 | 0 | 12 | 0 |
| **F** | 0 | 20 | 0 | 20 | * | 0 | 0 | 10 | 17 | 0 | 0 |
| **M** | 11 | 0 | 9 | 0 | 0 | * | 0 | 0 | 0 | 0 | 0 |
| **M** | 0 | 0 | 0 | 7 | 0 | 0 | * | 0 | 0 | 15 | 11 |
| **F** | 0 | 0 | 17 | 0 | 0 | 17 | 0 | * | 4 | 0 | 0 |

| | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| **F** | 11 | 7 | 8 | 0 | 17 | 0 | 10 | 0 | * | 10 | 10 |
| **F** | 0 | 0 | 17 | 0 | 0 | 0 | 8 | 0 | 0 | * | 0 |
| **M** | 0 | 0 | 0 | 0 | 0 | 0 | 14 | 20 | 0 | 8 | * |

**P 2004**

| | **F** | **M** | **M** | **F** | **F** | **F** | **M** |
|---|---|---|---|---|---|---|---|
| **F** | * | 14 | 9 | 24 | 22 | 14 | 6 |
| **M** | 8 | * | 18 | 35 | 18 | 10 | 0 |
| **M** | 4 | 18 | * | 45 | 20 | 8 | 0 |
| **F** | 0 | 4 | 13 | * | 26 | 8 | 0 |
| **F** | 17 | 14 | 8 | 31 | * | 22 | 0 |
| **F** | 3 | 5 | 6 | 8 | 24 | * | 0 |
| **M** | 3 | 0 | 0 | 14 | 17 | 33 | * |

**PO 2004**

| | **M** | **F** | **F** | **M** | **F** | **F** | **M** |
|---|---|---|---|---|---|---|---|
| **M** | * | 7 | 3 | 18 | 14 | 0 | 17 |
| **F** | 12 | * | 19 | 4 | 14 | 0 | 0 |
| **F** | 18 | 11 | * | 10 | 8 | 25 | 15 |
| **M** | 27 | 4 | 7 | * | 13 | 0 | 20 |
| **F** | 6 | 5 | 15 | 16 | * | 0 | 6 |
| **F** | 0 | 0 | 75 | 0 | 0 | * | 0 |
| **M** | 10 | 0 | 31 | 3 | 14 | 0 | * |

**P 2005**

| | **F** | **M** | **F** | **F** | **M** | **F** | **F** | **F** | **F** |
|---|---|---|---|---|---|---|---|---|---|
| **F** | * | 21 | 20 | 20 | 28 | 15 | 17 | 20 | 50 |
| **M** | 8 | * | 17 | 15 | 26 | 19 | 0 | 3 | 50 |
| **F** | 5 | 0 | * | 12 | 6 | 8 | 19 | 0 | 20 |
| **F** | 10 | 15 | 14 | * | 29 | 10 | 11 | 11 | 46 |
| **M** | 6 | 25 | 25 | 13 | * | 13 | 0 | 13 | 20 |

| | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| **F** | 3 | 28 | 13 | 7 | 12 | * | 2 | 4 | 22 |
| **F** | 6 | 4 | 67 | 17 | 5 | 10 | * | 22 | 15 |
| **F** | 17 | 45 | 120 | 20 | 22 | 24 | 17 | * | 29 |
| **F** | 18 | 33 | 0 | 12 | 47 | 0 | 31 | 12 | * |

**PO 2005**

| | **M** | **F** | **F** | **M** | **F** |
|---|---|---|---|---|---|
| **M** | * | 3 | 13 | 26 | 11 |
| **F** | 9 | * | 3 | 24 | 63 |
| **F** | 33 | 9 | * | 43 | 30 |
| **M** | 11 | 11 | 27 | * | 16 |
| **F** | 6 | 10 | 16 | 13 | * |

**Figure S5:** Normalized David's scores plotted against rank order (calculated from unreciprocated allogrooming hierarchies) for the individuals of group P 2005 that displayed a significantly linear, steep unreciprocated allogrooming hierarchy.