Grooming, Group Size and Language: No Links - A Reply to Dunbar & Lehmann (2013)

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The main inspiration for doing the analyses of grooming in relation to group size was the claim (Dunbar 1993) that available grooming time may become limiting and thus constrain group size in primates when grooming time must keep up with increased group size, and that our hominin ancestors, confronted with this problem, resorted to language as a way to service multiple social bonds simultaneously. (Dunbar and Lehmann 2013) argued that the suggestion that language is the functional equivalent of social grooming in primates has been refuted anyway, thus largely removing the need for the analysis. We agree with them, except that we maintain that the analysis in Grueter et al. (2013), questioned by Dunbar & Lehmann (2013), has shown that the logic underlying the original hypothesis was unsound.

The main point of our paper (Grueter et al. 2013) was that grooming for hygiene was strongly favored by terrestriality, which leads to higher parasite loads and dirt loads in the fur, and that the social function of grooming could become especially elaborate in species where the grooming tendency was high to begin with due to terrestriality. Using a large sample of primates while also controlling for phylogenetic non-independence among species and body size, we found clear and consistent support for terrestriality, but a weak or non-significant group size effect. Moreover, a number of intra-population analyses, which are very powerful due to the absence of any ecological confounds, failed to demonstrate a group size effect.

Dunbar and Lehmann (2013) provide a list of suggestions why they believe this conclusion is incorrect and that group size remains the best driver of grooming time among primates, as in their previous articles (Dunbar 1991; Lehmann et al. 2007a). Here we offer the arguments that lead us to stand by our conclusions.

First, (Dunbar and Lehmann 2013) claim that we rediscovered a significant effect of group size on grooming time. Let us reiterate: grooming time was not significantly predicted by group size within primates as a group when considering actual grooming partners, but the result was marginally significant when including potential grooming partners. We believe that actual grooming partner is the more apt measure of group size here (see below). A breakdown by major taxonomic groups shows no relationship of the two variables in Cercopithecopidea (largest sample!) and a negative relationship in platyrrhines (where substrate was not a confound, since all taxa are arboreal). The negative association in platyrhines confirms that the group size effect reported by (Dunbar 1991; Lehmann et al. 2007a) is a terrestriality effect, i.e. terrestrial species tend to live in larger groups (using our sample: Mann Whitney U, $Z = -3.744$, $p < 0.0001$), so grooming time is not driven by group

size per se, but by terrestriality. The only taxon for which we did find a positive relationship between group size and grooming was the apes, and this requires explanation.

Second, (Dunbar and Lehmann 2013) argue that there are two species whose group sizes are outliers, viz. *Colobus angolensis* and *Papio papio*. While scouring the primate literature, we included every study that reported group size and grooming time for the same population while adhering to additional inclusion criteria outlined in (Grueter et al. 2013) (e.g. wild and unprovisioned populations; data on actual grooming time, not time spent socializing). The Nyungwe population of *C. angolensis* that we included was the only population for which data on both activity budgets (grooming time) and group size have been published. As for *P. papio*, (Sharman 1981)'s study is the only one that reports data on grooming and group size. Recent research effort devoted to this species indicates that they exhibit a fluid organization with a mean party size of 16 (Patzelt et al. 2011). Assuming that the relatively high grooming value by Sharman (8.3%) is adequate, replacing Sharman's value for group size (192.5) with Patzelt et al. (2011)'s more recent estimate for party size (16) would have weakened the overall fit of the grooming-group size model.

Third, (Dunbar and Lehmann 2013) contend that we have not chosen the correct grouping level in species with multilevel societies and fission-fusion dynamics by focusing on the actual groups or parties. In multilevel societies, affiliative behaviour is largely restricted to the nuclear one-male unit and grooming involving members of different one-male units is an exceptionally uncommon phenomenon (Dunbar and Dunbar 1975; Grueter 2009; Grueter et al. 2012; Kummer 1990; Zhang et al. 2012). Using band as the level of analysis would thus have been a breach of logic; besides, bands in some multilevel taxa may not even constitute real individualized societies, as attested to by the limited individual recognition in gelada bands (Bergman 2010). Moreover, if the mere presence of other social

71 units in the vicinity elicited more bonding, then we would also expect an influence of home
72 range overlap (as a proxy for inter-group encounter rate and conflict potential), but there is no
73 evidence for that (Grueter 2013). Foraging party size was used only for species with fission-
74 fusion dynamics (chimpanzees, bonobos) and not for species with modularity where core
75 units never split into smaller subunits. In chimpanzees and bonobos, the whole community is
76 rarely physically assembled (Goodall 1986; White 1996), so the average number of
77 individuals from which to choose is best indexed by the size of the foraging party. After all,
78 one can only groom someone who is present. Finally, (Dunbar and Lehmann 2013) also state
79 that the foraging unit in groups characterized by fission-fusion is an alternative response to
80 socioecological stress (Lehmann et al. 2007b), thus bypassing the need for building strong
81 coalitions by means of grooming – the latter being the typical means by which group
82 cohesion is achieved (see also comment below). If this is the case, then the use of community
83 size in the analyses is unjustified as the act of temporary fissioning has removed the need for
84 grooming.

85 Fourth, (Dunbar and Lehmann 2013) question our understanding and interpretation of
86 the role of grooming in a social context. To begin with, we have never claimed that grooming
87 is solely hygienic and does not serve any social functions. We have clearly acknowledged the
88 various social benefits that primates derive from grooming and have argued that these social
89 functions (gaining social tolerance; relationship maintenance and access to valuable services
90 and resources, eg. (Henzi and Barrett 1999; Schino 2007; Yu et al. 2013)) were co-opted
91 where grooming need (such as in ground-dwelling primates) was high. However, the main
92 group cohesion mechanism proposed by (Dunbar 1991), i.e. investing more allogrooming
93 time in allies, does not seem to receive strong support ((Di Bitetti 2000), but see (Kudo and
94 Dunbar 2001). Also, there are plenty of primate species that never form coalitions and
95 nonetheless engage in grooming. Furthermore, (Dunbar and Lehmann 2013) maintain that

platyrhines live in groups small enough not to need grooming (for coalition formation), but then we should see similarly low rates of grooming in small groups of Old World monkeys etc. The claim that platyrhines do not use grooming as a bonding mechanism seems flawed in light of the available counterevidence (eg. (Di Bitetti 1997).

Fifth, (Dunbar and Lehmann 2013) were surprised that we considered fewer variables than they did in their analysis (Lehmann et al. 2007a). They found that female dispersal had a stronger effect on grooming time than terrestriality, and that terrestriality did not affect grooming time independently of female dispersal. In our dataset, however, grooming time differed significantly between arboreal and terrestrial species (ANOVA, $F = 31.556$, $p < 0.0001$, $n = 73$; Fig. 1), and the strong effect of terrestriality persisted if other predictors were included in the model (Grueter et al. 2013). Initially, we included a number of other potential predictors such as brain size, group structure (multi-male vs. one-male groups), and dispersal patterns in the models, but they did not exert a significant effect on grooming time. Although we also find a weak correlation between terrestriality and female dispersal (chi square likelihood ratio = 3.292, $p = 0.0696$, $n = 62$), female dispersal is not a significant predictor of grooming time if terrestriality is included in the model (PGLS: R^2 adj. = 0.294, $n = 61$, lambda = 0.251; female body mass: effect = -2.26, $p = 0.014$; terrestriality: effect = -8.58, $p < 0.0001$; dispersal: effect = 1.065, $p = 0.475$). Given the importance that (Dunbar and Lehmann 2013) attach to female dispersal, we should have reported the absence of these effects in our paper, but this would not have affected our conclusions. (Dunbar and Lehmann 2013) also assert that a simple dichotomous variable like terrestriality as a measure of parasite load is not ideal as some of the most terrestrial of all the primates (e.g. the gelada) inhabit open grassland that is almost free of ticks and other parasites. This is an interesting point, but terrestriality does not only reflect greater parasite loads, but also greater exposure to dirt particles and accordingly skin irritation (Ungar 1994).

Sixth, (Dunbar and Lehmann 2013) note that in neither of their analyses, nor in our analysis, does grooming time correlate with body mass. However grooming does correlate with body mass in our analyses when looking at primates as a whole (negatively related), although there was variation among taxonomic groups (Grueter et al. 2013). As body surface scales negatively allometric with mass, parasite load is less intense for larger species, so the negative correlation is not unexpected.

Seventh, the reason why we made no mention of Lehmann et al. (2007a)'s "intra-specific comparisons" is because their within-*taxon* analyses are not comparable with our within-*population* analyses; the latter are much more powerful because all groups stem from the same population and face largely similar ecological conditions, allowing us to obtain an unbiased 'ecologically neutral' estimate of the importance of group size on grooming.

Taken together, these arguments and analyses corroborate our earlier conclusion that the link between social grooming and group size/cohesion in primates is weak at best. This removes the functional basis for the 'grooming-as-language' hypothesis, but also for the hypothesis that primate group size is limited by grooming time (Dunbar 1993) rather than scramble competition for food (Janson and Goldsmith 1995) or infanticide avoidance (Steenbeek and van Schaik 2001).

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213 **Fig. 1.** Differences in the percentage of time spent allogrooming between arboreal (A) and
214 terrestrial (T) primate species. The center lines of the mean diamonds are the group means
215 and the vertical endpoints form the 95% confidence interval for the mean (Sall et al. 2005).

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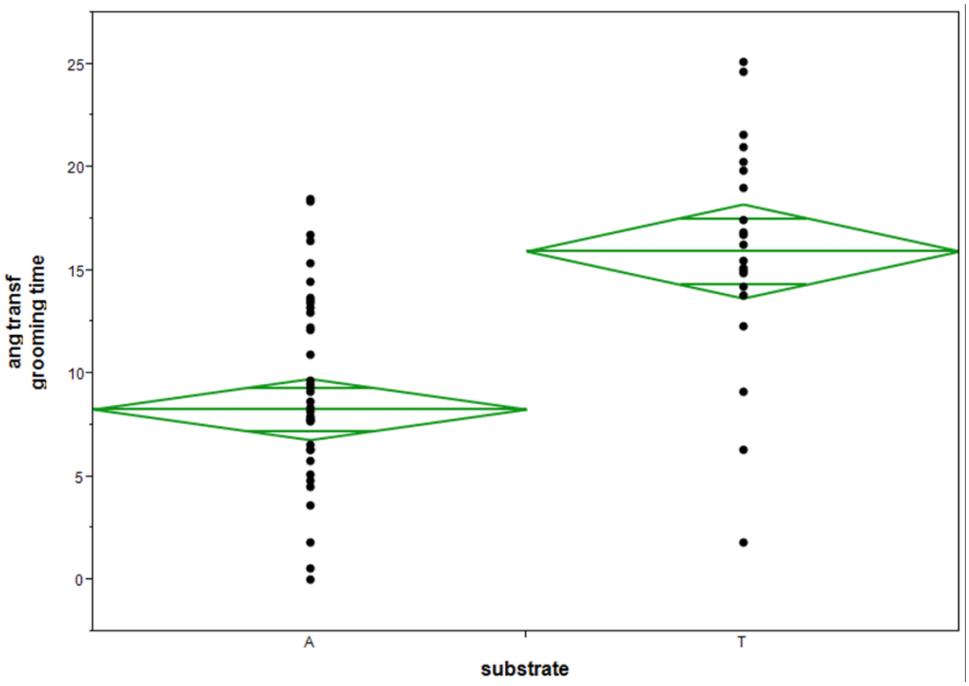

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