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Research article

Behavioural changes in response to changing group size and sex ratio in a captive bonobo *Pan paniscus* group

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Abstract
In modern zoological organisations, the size and sex ratio of great ape groups are determined by management recommendations that aim to replicate the dynamics of wild groups. In this study, the influence of changing group size and sex ratio on the behaviour of a captive group of bonobos *Pan paniscus* is investigated. It was found that group size and sex ratio significantly influenced the occurrence of genito-genital rubbing while grooming, social play, stereotypy, locomotion and agonistic behaviours were not found to be significantly impacted either by group size or sex ratio. Authors suggest that in this case genito-genital rubbing is sufficient to mitigate social tensions brought about by the comparatively small changes in group composition occurring in this study. These results indicate the importance of both group size and sex ratio on the daily behaviour of captive bonobos and suggest that they should be taken into account when managing the fission-fusion dynamics of captive bonobo groups.

Introduction

Many mammal species are group-living (Kappeler and van Schaik 2002; Silk 2007). The benefits of living in a group may include higher access to mates, protection from predators and more foraging opportunities (Kappeler and van Schaik 2002; Silk 2007). The African great apes, bonobos *Pan paniscus*, gorillas *Gorilla gorilla* and chimpanzees *Pan troglodytes* live in social groups of varying sizes and structures (Parnell 2002: Furuichi 2009). The size of a wild great ape group is determined by nutritional needs, predation risk and proximity to potential mates (Wrangham 1996). In the wild, intra-group competition for food can limit group size (Dunbar 2020) whereas in captivity, food availability is no longer a limiting factor. However, in captivity, great apes occupy far smaller areas than they would in the wild (Ross and Shender 2016) which may exacerbate social tensions. Equally, the number of possible social partners is also considered an important factor in the welfare of captive great apes due to the stimulating dynamic social opportunities they provide (Lehmann et al. 2007; Neal Webb et al. 2019: Fultz et al. 2022). For example, larger groups of captive chimpanzees have been observed to spend more time carrying out social affiliative behaviours (Lehmann et al. 2007) and chimpanzee groups containing seven or more individuals exhibit more locomotion and social behaviours overall (Neal Webb et al. 2019). Group size also has longer term effects on behaviour, for instance, chimpanzee personality is influenced by the size of the group in which they were reared (Gartner and Weiss 2018).

In the case of the bonobo, there is much less knowledge available concerning the species in comparison to the other great apes, particularly in regard to zoo husbandry (Gruber and Clay 2016; Laméris et al. 2021). The zoo-housed population of bonobos in European institutions is likely to grow through the management of the international breeding programme (Guzen 1975; van Coillie et al. 2008). Consequently, more institutions are likely to become holders of this species in the near future for the first time. With this inevitability of new captive bonobo groups being formed, it is essential that knowledge is available regarding the impacts of group size and sex ratio on bonobo behaviour and welfare. This key information can be used alongside current knowledge when assigning the number and sex ratio of a new bonobo group when aiming to optimize welfare. The following study focuses on the effects of group

size (number of individual bonobos present in a group) and sex ratio (measured as percentage of females) on the behaviour of captive bonobo group.

Wild bonobos tend to live in larger groups than chimpanzees (Mulavwa et al. 2008) and, like chimpanzees, bonobos have a dynamic social system of groupings that divide and reform on a regular basis known as fission-fusion (Badrian and Badrian 1984; Furuichi 2011). The size of a group of bonobos has been found to positively correlate to food availability and can range between a lone individual to subgroups of 20 (Badrian and Badrian 1984) within a larger community (Samuni et al. 2022). In the case of captive bonobos, the EAZA Best Practice Guidelines recommend that new enclosures are built for a minimum of 10 adults. At the time of writing the median group size of bonobos within the EEP (European Endangered Species Programme) is 13 individuals and the median group size for the Species Survival Plan (SSP) is 11. When housed under crowded conditions bonobos have previously been found to exhibit higher affiliative behaviours but also increased incidence of aggression (Sannen et al. 2004). Likewise, increased sociosexual contact and social play following the addition of more group members has been observed in this species (Caselli et al. 2023).

Sex ratio is also known to impact the behaviour of great ape groups. In chimpanzees, an increased number of adult males present in a group increases the incidence of aggression and conflict due to the high male-male aggression typical of this species (Price and Stoinski 2007) whereas in gorillas, aggression appears to be highest in males aged 14-20 compared to other age-sex classes (Robbins et al. 2004; Breuer et al. 2009). In wild bonobos, as the group size increases, the percentage of adult females present also tends to increase (Badrian and Badrian 1984). This is suggested to be due to the importance of adult female alliances in bonobo society (Franz 1999; Paoli et al. 2006; Anzà et al. 2021). In bonobos, adult females have the highest social status (Franz 1999) and tend to exhibit more affiliative social behaviour than male bonobos (Badrian and Badrian 1984; Staes et al. 2017). In particular, females exhibit more frequent genito-genital rubbing, a behaviour used to reconcile following group tension (Paoli et al. 2006; Anzà et al. 2021). Furuichi (2011) suggests that the close associations formed by females results in more affiliative social behaviour between them. More recently, Mouginot (2024) has found that the incidence of aggression in male bonobos is as high as in male chimpanzees, though is less intense. As a result, we expect the sex ratio of a bonobo group to impact the overall group behaviour.

This study investigates a group of bonobos that are managed by artificial fission-fusion which allows the regular division and reformation of bonobo groups resulting in groups of different sizes and sex ratios with the same individuals. Here, aggressive, affiliative and stress-related behaviours are examined in response to changing group size and sex ratio in a bonobo group housed at The East Midland Zoological Society Twycross Zoo (Twycross Zoo). We make the following predictions:

1) The incidence of the affiliative social behaviours; grooming, play and genito-genital rubbing is expected to increase with group size and percentage of females present.

2) The incidence of agonistic behaviours is expected to increase with group size and expected to decrease with percentage of females

3) The incidence of locomotion is expected to increase with group size and percentage of females present.

4) The incidence of stereotypical behaviours is expected to change with group size.

Methods

Study subjects and data collection

The study was conducted between the 3 March 2023 and 24 July 2023 at Twycross Zoo using non-invasive behavioural observations on the 14 resident bonobos (Sex ratio 6:8) (see Appendix 2). The bonobos are housed in two groups at all times with individuals regularly transferred every one to seven days between groups as part of their fission-fusion management. The group size ranged from five to nine individuals. The proportion of females present in each group (ranging from 0.25 to 0.83) was used to investigate the impacts of sex ratio. A total of 225 30-minute observations were collected for this study (n=112.5 hours). Each group was surveyed using scan sampling (Altmann 1974) for 30 minutes at three-minute intervals using an ethogram created to reflect this groups common behaviours (See Appendix 3). In addition, all-occurrence data were collected for genito-genital rubbing behaviour (see Appendix 3) which was selected as an important indicator of social tension but can be too brief to be captured by interval scanning. Observations were undertaken during the hours of 1000-1300 and 1400-1530 which were periods that did not coincide with animals feeding and husbandry routines. Observations were not taken during the transfers of bonobos from one group to another. Surveys were carried out by a team of seven bonobo keepers who can individually identify the research subjects. Interobserver reliability was ensured by observers carrying out an observation session on a film of footage showing bonobos exhibiting the behaviours listed in the ethogram and comparing answers to the most experienced observer. Interobserver agreement was 85% or more for each observer. Surveys were recorded on tablets in public areas using the Zoomonitor Software. The behaviour of each individual was recorded at each interval. The data collected are purely observational in nature and the research project was approved by Twycross Zoo's Research Ethics Committee.

Enclosure

The bonobos are housed in an enclosure with two indoor areas and two outdoor areas with six off show areas available on the left-hand side and four on the right-hand side of the enclosure. The bonobos are housed in two groups on either side of the building allowing for a large indoor, outdoor and off-show area for each group. Individuals are regularly transferred by keepers to the neighbouring group to mimic fission fusion dynamics.

Statistical Analysis

Behaviour was analysed at an individual level. Data were analysed using R Version 4.2.2 in the RStudio software (R Core Team 2020) using "lme4"and "ggeffects" packages. Genito-genital rubbing was analysed using all-occurrence data due to the brevity of these behaviours meaning it was not easily captured by scan sampling. This was quantified as count data and was analysed using a poisson generalized linear model (GLM) with genito-genital rubbing expressed as number of occurences per 30 minute observation session. The poisson distribution was used for short behaviours (e.g. gg-rubbing) and were recorded as all occurrence points. The binomal distribution was used for the behaviours collected by scan sample.

Social play, stereotypical behaviours, grooming and locomotion were analysed using scan sample data. These behaviours were quantified as percentage of total activity budget during a 30 minute observation session. Generalised linear models (GLMs) with a binomial distribution were fitted for these behaviours.

The side of enclosure in which the bonobos were housed was initially included in the model to mitigate for slight variations in size of areas but was not found to have a significant effect so was excluded from the models. All behaviours were analysed in response to group size and percentage of females.

Table 1. Average activity budget and occurrence of behaviours for each group size to two decimal places

	Agonistic	Grooming	Locomotion	Play	Stereotypy	GG-rubbing (All-occurrence)
Group Size	Mean %	Mean %	Mean %	Mean %	Mean%	Mean frequency per 30 minute observation session
5	0.09	21.04	6.05	1.98	0.17	0.07
6	0.41	20.16	9.33	2.33	0.54	0.09
7	0.29	22.30	6.67	3.26	0.04	0.04
8	0.43	23.35	11.87	2.78	0.17	0.08
9	0.12	15.18	7.92	7.89	0.69	0.14
Overall	0.32	21.07	9.03	3.53	0.29	0.08

Results

Descriptive statistics

In order to test for differences caused by group size, the average proportion of activity budget allocated to each target behaviour (locomotion, play, stereotypy, grooming, agonistic) and the average frequency of all occurrence behaviour (genito-genital rubbing) was calculated. Likewise, the proportion and occurrence of behaviours were calculated for each percentage of females present. The mean for each behaviour in response to group size and sex ratio is detailed below in Table 1 and Table 2.

Group size

Behaviours locomotion, play, stereotypy, grooming, agonistic and genito-genital rubbing were analysed in response to group size (Table 3 and Figure 1). The size of the bonobo groups ranged from 5 to 9 individuals. A greater number of individuals in a group resulted in significantly more occurrences of genito-genital rubbing. Locomotion, social play, agonistic, grooming and stereotypical behaviours were not found to be significantly influenced by group size.

Percentage of female bonobos present in a group ranged between 25% and 83% during this study. A higher proportion of female bonobos present in a group resulted in the occurrence of significantly more genito-genital rubbing (Table 4, Figure 2). Locomotion, social play, agonistic behaviours and stereotypies were not found to be significantly influenced by percentage of females present.

Discussion

In this study, the behavioural effects of alterations in group size and sex ratio were investigated. Genito-genital rubbing was found to have a significant positive association with both group size and percentage of females present which is consistent with the findings of Sannen et al. (2004). However, in this case, agonistic behaviour was not significantly affected by group size or percentage of females. Since genito-genital rubbing is a reconciliatory response to social tension in a bonobo group (Paoli et al. 2006) it is possible that this affiliative behaviour was sufficient to mitigate the amount of agonistic behaviour exhibited. This supports the suggestion that bonobos are adopting a conflict-avoidance strategy in response to more group mates (de Waal and Aureli 1997).

Table 2. Average activity budget and occurrence of behaviours for each proportion of females to two decimal places.

	Agonistic	Grooming	Locomotion	Play	Stereotypy	Average Rate of GG-rubbing
Proportion of Females	Mean %	Mean %	Mean %	Mean %	Mean %	Mean frequency per 30 minute observation session
37.5%	0.31	12.19	13.85	3.33	0.4617	0.02
40%	0	6.67	7.78	1.11	0	0
44.4%	0.15	14.24	8.02	8.40	0.84	0.097
50%	0.30	34.23	7.41	2.29	0.75	0.01
57.1%	0.35	8.54	7.85	3.84	0.05	0.04
62.5%	0.68	4.55	14.58	3.34	0	0.15
66.7%	0	43.24	5.26	4.01	0	0.48
80%	0.14	0	7.51	2.81	0.27	0.08
83.3%	0.55	5.47	11.56	2.08	0.08	0.2

Table 3. Results of GLMs for the effect of group size on the occurrence of bonobo behaviours. Significant P values of less than 0.05 are marked with a *.

Behaviour	Estimate	Standard Error	Z Value	Pr(>|Z|)
Stereotypical Behaviours	-0.9393	1.5719	0.598	0.550
Locomotion	0.04475	0.030582	0.146	0.884
Grooming	-0.1391	0.2265	-0.614	0.5393
Social Play	0.799	0.4994	1.602	0.1092
Genito-genital Rubbing	1.4165	0.4113	3.444	<0.05*
Agonistic	-0.6602	1.6497	-0.400	0.689

As a female dominated species, having proportionally fewer females present could result in a reduction in social stability (Moscovice et al. 2017; Yokoyama and Furuichi 2023). In addition, bonobos have also been known to employ grooming as a conflict-avoidance strategy (Van Dyck et al. 2003) and therefore we may expect to observe more grooming behaviour in response to increased social tension caused by a greater proportion of males similar to what is found in chimpanzees (Price and Stoinski 2007). However, in this case no significant result was found between grooming and sex ratio.

Palagi and Paoli (2007) suggest that social play is used to assess and strengthen relationships by bonobos and is used as a low-risk way of determining hierarchy and alliances within the group. Therefore, we would expect that social play increases as the group

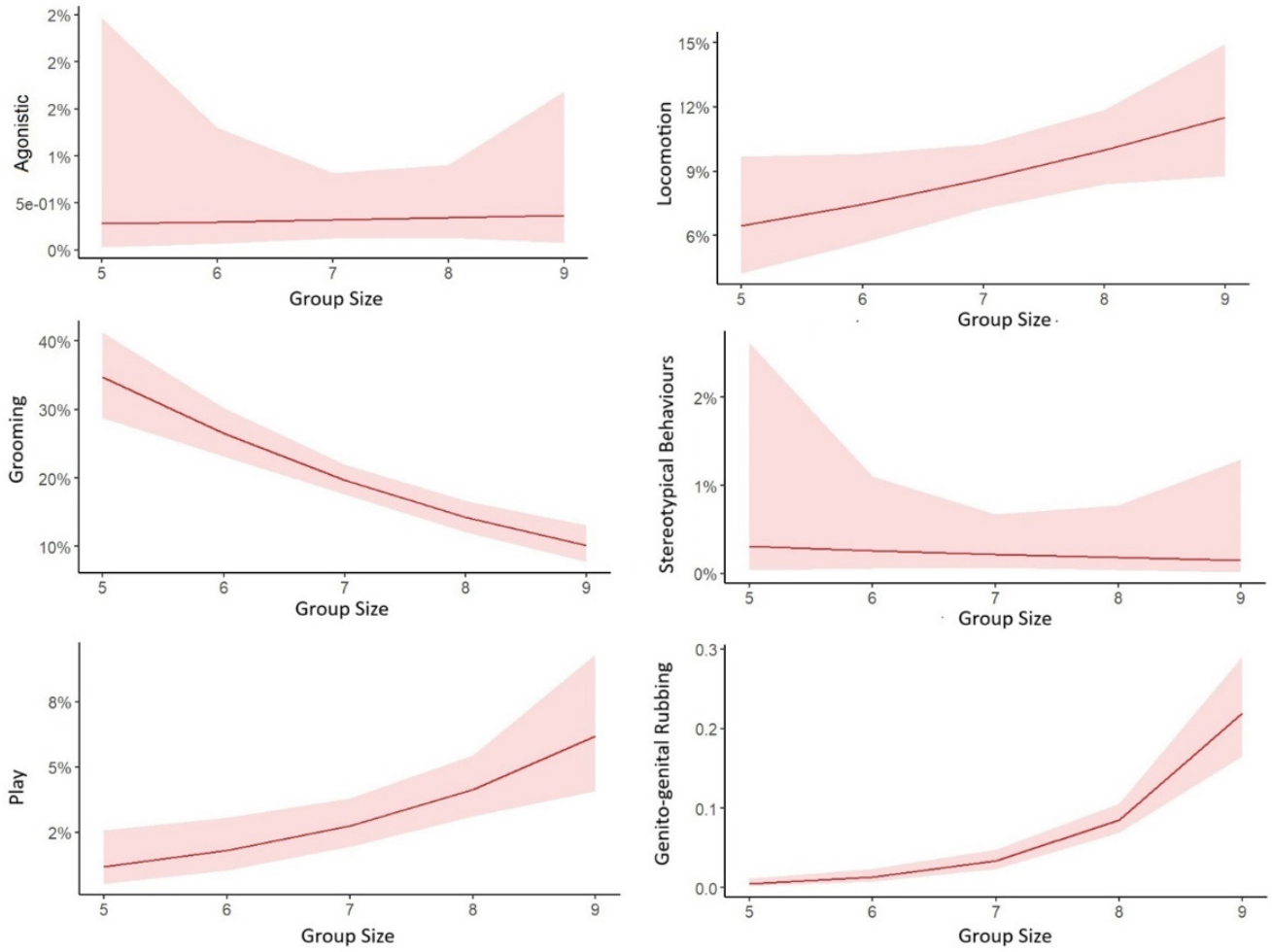

Figure 1. Graphs show quantity of behaviours in response to increasing group size with shaded areas denoting standard error. Behaviours shown in response to group size are agonistic (P>0.05), locomotion (P>0.05), grooming (P>0.05), stereotypical behaviours (P>0.05), social Play (P>0.05 and genito-genital rubbing (P<0.05).

Table 4. Results of GLMs for the effect of percentage of females present on the occurrence of bonobo behaviours. Significant P values of less than 0.05 are marked with a *.

Behaviour	Estimate	Standard Error	Z Value	Pr(>|Z|)
Stereotypical Behaviours	9.6697	20.6316	0.469	0.639
Locomotion	-0.08092	3.65212	-0.022	0.982
Grooming	-3.5016	3.0299	-1.156	0.2478
Social Play	5.8387	6.1913	0.943	0.3457
Genito-genital Rubbing	15.1492	4.4998	3.367	<0.05*
Agonistic	-6.4820	18.6779	-0.347	0.729

size increases because there are more relationships to maintain. However in this case no statistically significant relationship was found between social play and group size or percentage of females.

Group size had no effect on stereotypical behaviour suggesting that the number of partners in this range (5 to 9 individuals) of group sizes is not a stressor to this group of bonobos. Likewise, locomotion was not found to be significantly affected by either group size or percentage of females. Wild ape communities tend to travel more when they are in larger groups (Lehmann et al. 2007), a tendency which is largely attributed to food competition which could explain the lack of significance in this case as sufficient food is provided in captivity.

Limitations of this study include interaction between groups since they are housed in the same building and have visual,

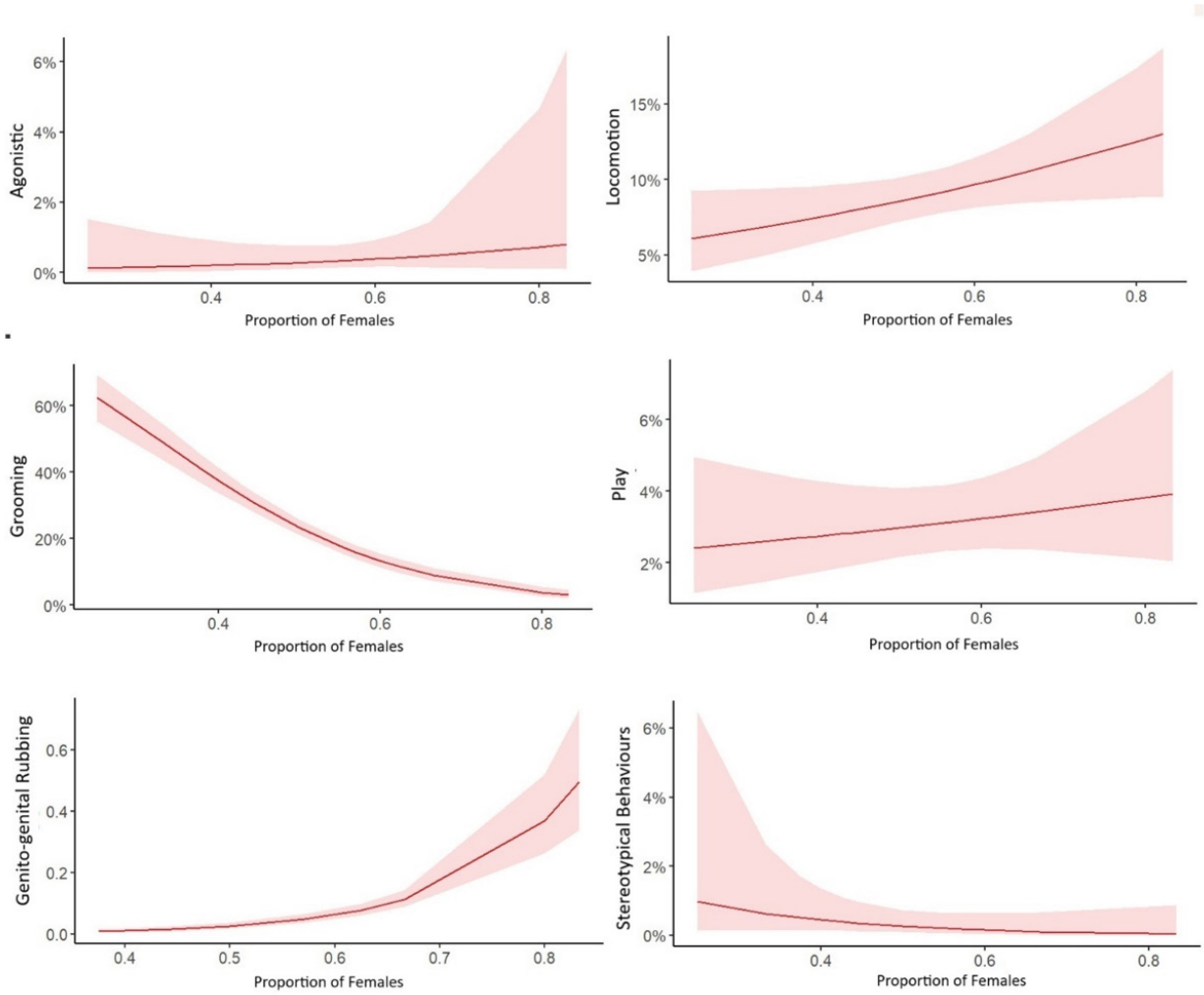

Figure 2. Graphs show quantity of behaviours in response to increasing percentage of females with shaded areas denoting standard error. Behaviours shown in response to group size are agonistic (P>0.05), locomotion (P>0.05), grooming (P>0.05), stereotypical behaviours (P>0.05), social Play (P>0.05 and genito-genital rubbing (P<0.05).

olfactory and auditory access to one another allowing for interaction even when housed in separate groups. Recently published research (van Leeuwen et al. 2024) has found that there is significant variation in behaviour between bonobo groups therefore patterns identified in this study may be particular to the group studied. Further research from multiple groups managed with fission-fusion would give further insight into whether the patterns of significance found here are typical across captive bonobo groups. Furthermore, certain short behaviours such as antagonism may have been under sampled due being observed using scan methods rather than all occurrence. Also, in this instance we have controlled for individual bonobo but a future direction for this study would be to investigate the effect of dominance rank and age on group behaviour.

Conclusion

In this study we have found that the Twycross bonobo group responds to changes in sex ratio and group size by exhibiting genital rubbing behaviour. Unexpectedly, group size and sex ratio did not significantly impact any other social behaviours which contradicts the previous studies mentioned above. It is possible that the changes in group dynamics caused by change in group size and sex ratio were minor enough that genito-genital rubbing alone was sufficient to mitigate any tension. Alternatively it is possible that this particular group has a higher reliance on genito-genital rubbing as a method for mitigating social tension. Therefore, we suggest that further research including multiple bonobo groups is required to determine suitable and unsuitable group parameters for captive bonobos. Further research is needed to determine the most appropriate sex ratio and we suggest that it is taken into consideration when housing this species. Since fission-fusion management is already carried out, this study provides further information to bonobo caregivers and zoo management when selecting individuals for fission-fusion and for selecting individuals for permanent relocation when aiming to create a bonobo group that behaves as naturally as possible.

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References

Altmann, J. (1974). Observational study of behavior: sampling methods. *Behaviour* 49(3-4), 227-266.

Anzà S., Demuru E., Palagi, E. (2021). Sex and grooming as exchange commodities in female bonobos' daily biological market. *Scientific Reports* 11(1): 19344.

Badrian A., a Badrian N. (1984). Social organization of *Pan paniscus* in the Lomako Forest, Zaire. In: Susman, R.L. (ed.) *The Pygmy Chimpanzee: Evolutionary Biology and Behavior*. Boston, MA: Springer US, 325-346.

Breuer T., Hockemba M.B.N., Olejniczak C., Parnell R.J., Stokes E.J. (2009). Physical maturation, life-history classes and age estimates of free-ranging western gorillas—Insights from Mbeli Bai, Republic of Congo. *American Journal of Primatology* 71(2): 106-119.

Caselli, M., Malaman, B., Cordoni, G., Guéry, J.P., Kok, J., Demuru, E., Norscia, I. (2023). Not lost in translation: Changes in social dynamics in Bonobos after colony relocation and fusion with another group. *Applied Animal Behaviour Science* 261; 105905.

de Waal F.B., Aureli F. (1997). Conflict resolution and distress alleviation in monkeys and apes. *The Integrative Neurobiology of Affiliation* 807: 317-328.

Dunbar R.I.M. (2020). Structure and function in human and primate social networks: Implications for diffusion, network stability and health. *Proceedings of the Royal Society A* 476(2240): 20200446.

Franz C. (1999). Allogrooming behavior and grooming site preferences in captive bonobos (*Pan paniscus*): association with female dominance. *International Journal of Primatology* 20(4): 525-546.

Furuichi T. (2009). Factors underlying party size differences between chimpanzees and bonobos: a review and hypotheses for future study. *Primates* 50: 197-209.

Furuichi T. (2011). Female contributions to the peaceful nature of bonobo society. Evolutionary Anthropology: Issues, News, and Reviews 20(4): 131-142.

Gartner M.C., Weiss A. (2018). Studying primate personality in zoos: Implications for the management, welfare and conservation of great apes. *International Zoo Yearbook* 52(1): 79-91.

Guzen, A. (1975). Studbook of *Pan paniscus* Schwarz, 1929. *Acta Zoologica et Pathologica Antverpiensia* 61: 119-164.

Gruber T., Clay Z. (2016). A comparison between bonobos and chimpanzees: a review and update. *Evolutionary Anthropology: Issues, News, and Reviews* 25(5): 239-252.

Kappeler P.M., van Schaik C.P. (2002). Evolution of primate social systems. *International Journal of Primatology* 23: 707-740.

Laméris, D.W., Staes, N., Salas, M., Matthyssen, S., Verspeek, J., Stevens, J.M. (2021). The influence of sex, rearing history, and personality on abnormal behaviour in zoo-housed bonobos (*Pan paniscus*). *Applied Animal Behaviour Science* 234: 105178. https://doi.org/10.1016/j.applanim.2020.105178

Lehmann J., Korstjens A.H., Dunbar R.I. (2007). Fission–fusion social systems as a strategy for coping with ecological constraints: a primate case. *Evolutionary Ecology* 21: 613-634. https://doi.org/10.1007/s10682-006-9141-9

Moscovice L.R., Douglas P.H., Martinez-Iñigo L., Surbeck M., Vigilant L., Hohmann G. (2017). Stable and fluctuating social preferences and implications for cooperation among female bonobos at LuiKotale, Salonga National Park, DRC. *American Journal of Physical Anthropology* 163(1): 158-172.

Mouginot, M., Wilson, M. L., Desai, N., Surbeck, M. (2024). Differences in expression of male aggression between wild bonobos and chimpanzees. *Current Biology* 34(8): 1780-1785.

Mulavwa M., Furuichi T., Yangozene K., Yamba-Yamba M., Motema-Salo B., Idani G. I., Mwanza N. (2008). Seasonal changes in fruit production and party size of bonobos at Wamba. In: Furuichi T., Thompson J. (eds.) *The Bonobos: Behavior, Ecology, and Conservation.* New York, NY: Springer US. pp. 121-134.

Neal Webb, S.J., Hau, J., Schapiro, S.J. (2018). Captive chimpanzee (*Pan troglodytes*) behavior as a function of space per animal and enclosure type. *American Journal of Primatology* 80(3): e22749.

Palagi E., Paoli T. (2007). Play in adult bonobos (*Pan paniscus*): modality and potential meaning. *American Journal of Physical Anthropology* 134(2): 219-225.

Paoli T., Palagi E., Tacconi G., Tarli S.B. (2006). Perineal swelling, intermenstrual cycle, and female sexual behavior in bonobos (*Pan paniscus*). *American Journal of Primatology* 68(4): 333-347.

Parnell R. (2002) The Social Structure and Behaviour of Western Lowland Gorillas (*Gorilla gorilla gorilla*) at Mbeli Bai, Republic of Congo. PhD Thesis. University of Stirling, UK

Price E.E., Stoinski T.S. (2007). Group size: Determinants in the wild and implications for the captive housing of wild mammals in zoos. *Applied Animal Behaviour Science* 103(3-4): 255-264.

R Core Team (2020). *R: A language and environment for statistical computing.* R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/.

Robbins M.M., Bermejo M., Cipolletta C., Magliocca F., Parnell R.J., Stokes E. (2004). Social structure and life-history patterns in western gorillas (*Gorilla gorilla gorilla*). *American Journal of Primatology* 64(2): 145-159.

Ross S.R., Shender M.A. (2016). Daily travel distances of zoo-housed chimpanzees and gorillas: implications for welfare assessments and space requirements. *Primates* 57: 395-401. https://doi.org/10.1007/s10329-016-0530-6

Sannen A., Elsacker L.V., Eens M. (2004). Effect of spatial crowding on aggressive behavior in a bonobo colony. *Zoo Biology* 23(5): 383-395.

Samuni, L., Langergraber, K.E., Surbeck, M.H. (2022). Characterization of Pan social systems reveals in-group/out-group distinction and out-group tolerance in bonobos. *Proceedings of the National Academy of Sciences* 119(26): e2201122119.

Silk, J.B. (2007). The adaptive value of sociality in mammalian groups. *Philosophical Transactions of the Royal Society B: Biological Sciences* 362(1480): 539-559.

Staes N., Eens M., Weiss A. Stevens J.M. (2017). Bonobo personality: Age and sex effects and links with behavior and dominance. In: Hare B., Yamamoto S., (eds.) *Bonobos: Unique in Mind, Brain and Behavior.* Oxford, UK: Oxford University Press , 183-198.

van Coillie S., Galbusera P., Roeder A.D., Schempp W., Stevens J.M.G., Leus, K Pereboom Z. (2008). Molecular paternity determination in captive bonobos and the impact of inbreeding on infant mortality. *Animal Conservation* 11(4): 306-312.

van Dyck S., Stevens J., Meuleman B., Elsacker L.V. (2003). Effects of the change in accommodation and group composition on the affiliative behaviour of a captive bonobo group (*Pan paniscus*). *Proceedings of the 5th Annual Symposium on Zoo Research,* Marwell Zoological Park, Winchester, UK, 7-8th July 2003 205-211.

van Leeuwen E.J., Staes N., Eens M., Stevens J.M. (2024). Group-level signatures in bonobo sociality. *Evolutionary Human Sciences* 6:, e48.

Wrangham R.W., Chapman C.A., Clark-Arcadi A.P., Isabirye-Basuta G. (1996) Social ecology of Kanyawara chimpanzees: implications for understanding the costs of great ape groups. In: McGrew W.C., Marchant L.F., Nishida T. (eds.) *Great Ape Societies*. Cambridge, UK: Cambridge University Press, 45-57.

Yokoyama T., Furuichi T. (2023). Partner choice in genito-genital rubbing among female bonobos (*Pan paniscus*) is highly dependent on physical proximity. *Primates* 64(1): 25-33.