Social proximities of developing gorilla males (Gorilla gorilla gorilla) in European zoos

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1   **Social proximities of developing gorilla males (*Gorilla gorilla* gorilla) in European zoos:**

2   **the consequences of castration and social composition.**

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18   **Abstract**

19   In the European captive population of western lowland gorillas (*Gorilla gorilla gorilla*), the

20   harem social structure and an even sex ratio at birth result in a surplus of males and

21   consequent management difficulties. This study seeks to assess the socialization differences

22   between captive juvenile and adolescent male gorillas according to their fertility status (intact

23   vs castrated) in different social compositions (familial vs bachelor groups), and to evaluate the

24   suitability of castration as a management tool for the EEP gorilla population. We carried out

25   social network analyses (SNA) to assess the "positive" proximity pattern of behaviour in 93

26   western lowland gorillas aged from 0 to 45 years old and housed in 11 social units (seven

27   familial and four bachelor groups). We compared the data recorded for the 27 juvenile and

28   adolescent (i.e. subadult and blackback) males included in our sample size. Although no

29   differences were revealed between the intact juveniles and the castrated juveniles living in

30   familial groups, our results showed that castrated adolescent individuals showed more

31   cohesiveness within their familial group than their intact conspecifics in terms of their activity

32   budget. They also displayed a "positive" proximity pattern of behaviour with all group

members, including adults (silverback and females). Despite being significantly more isolated, the intact adolescent males living in bachelor groups do not differ from their castrated and intact counterparts of the same age class living in familial groups in terms of their strength of "positive" behaviour when close to group conspecifics. This effect highlights the social benefits of male-male interactions within gorilla species. Our results may be evidence that both of the management strategies compared here, i.e. bachelor groups and castration, could be appropriate socio-behavioural enrichments during juvenility and adolescence. These findings also highlight the need to continue investigations until the study subjects reach adulthood to validate and/or improve these tools for the welfare-compliant management of gorilla male surplus in captivity.

Introduction

At the beginning of 2016, the EAZA (European Association of Zoos and Aquaria) ex-situ programme for gorillas (GEEP) comprised a total population of over 475 individuals in 74 institutions. Zoos have become successful in breeding western lowland gorillas, and they have considerably improved the captive management of this species over the years by sharing experience and knowledge that can help to improve daily husbandry (Ogden & Wharton, 1997; Stoinski et al., 2001; Strong et al., 2017).

However, the balanced sex ratio that naturally occurs at birth for this species and the long life of breeding males in captivity result in a problem of surplus males (Stoinski et al, 2013; Vermeer & Devreese, 2015; Vermeer et al., 2014). This male overpopulation has been managed by the creation of bachelor gorilla groups in zoos over the last three decades, namely through the application of previously published knowledge of wild mountain gorillas

1 (Johnstone-Scott, 1988; Pullen, 2005; Watts & Meder, 1996). Several factors including age,

2 early familiarity of individuals, group composition, number of males, exhibit design, rearing

3 experience and personality have already been identified as possible elements that play roles in

4 the successful formation and maintenance of captive multi-male gorilla groups (Coe, Scott, &

5 Lukas, 2009; Gold & Maple, 1994; Kuhar, Stoinski, Lukas, & Maple, 2006; Pullen, 2005; T.

6 S. Stoinski, Lukas, Kuhar, & Maple, 2004). In the European region, twenty gorilla bachelor

7 groups were established in 17 institutions between 1995 and 2015. A backward analysis of the

8 last two decades of bachelor group management in European institutions highlights social

9 instabilities that could be dangerous over time, such as aggressions and injuries. However,

10 recent studies on the North American captive gorilla population reported similar rates of

11 contact aggression shown by males in both familial and bachelor housing conditions. The

12 influence of young silverbacks was a strong confounding factor that increased both agonistic

13 behaviour and the wounding rate in the bachelor groups (Leeds et al., 2015; Stoinski et al.,

14 2013). These authors concluded that all-male groups could therefore be a long-term housing

15 strategy offering male gorillas the benefits of socialization if appropriate social grouping

16 prevents the risk of escalated aggression and the maintenance of affiliative relationships. As

17 early as 2001, the zoo community emphasized the importance of describing and studying how

18 adolescent blackback males or young silverback males change their social relationships with

19 the dominant silverback male as they grow older (Nakamichi & Kato, 2001). Indeed, key

20 predictors of social instability must be identified to prevent severe aggressive outbreaks in

21 bachelor groups when bachelor males become silverbacks. Likewise, knowledge of key social

22 stability predictors is also necessary to ensure that the affiliative relationships of young

23 individuals are maintained throughout maturation until adulthood. While our knowledge of

24 instability indicators for post-adolescent males and young silverbacks is increasing, very few

25 studies to date have investigated the stability indicators emerging from data collected on

younger individuals (juveniles and adolescents). Yet this information could be of crucial importance to guide management decisions attempting to control captive male overpopulation.

However, this bachelor group management strategy may not be sufficient to ensure the long-term relocation of future surplus males. The solutions that have been proposed and discussed include the use of sex ratio selection, a promising approach that requires further improvement. The Gorilla EEP (GEEP) has already reduced the number of females per breeding male to current levels of 2 or 3 at the most, thus providing a normal social upbringing for the offspring. Another proposal is to extend the time that young males remain in their natal group, or house them alone. This also appears to be impossible: blackback sub-adult transition is driven by intra-group competition, generally through unidirectional aggression exhibited by the silverback (Robbins, 2007), so remaining longer in their familial group will directly impact their well-being. It also appears unethical to house males alone in zoos, because this solution could impact individual welfare with more self-harming or abnormal behaviours such as hair plucking, regurgitation and reingestion, as reported for gorillas housed alone (Less et al., 2013). Although the use of euthanasia as a population management strategy would free up hosting capacities that could be used for housing other gorillas, this strategy is not recommended by the Great Ape TAG (Taxon Advisor Group), who limit its use to exceptional circumstances: "The Great Ape TAG accepts use of euthanasia for Great Apes in preference to keeping them long term under conditions which significantly reduce the individuals' welfare, and if there is no other alternative" (Abelló, Bemment, & Rietkerk, 2017 page 102). Castration meets this criteria (see Moreno Rivas and colleagues (2018) for additional explanations of the benefits of castration, such as improving genetic variability or reducing the potential drastic negative demographic effects due to an overuse of females contraception), and also reduces the cost of accommodation structures for this species. Given

1　the expense of creating new facilities for big mammals like gorillas, keeping the castrated

2　individuals in their familial group would also have financial advantages. For all these reasons,

3　the Gorilla EEP agreed to test the use of castration among males that were genetically over-

4　represented in the population as a supplementary tool to complement other, insufficient

5　management strategies. Castration at an early age is a possible management strategy insofar

6　that mature castrated males can remain in the presence of the silverback male in their native

7　familial group without the risk of conflicts, or can form part of a bachelor group without

8　competing for dominance. This study is a first step in this new EEP management strategy, and

9　focuses on young gorillas in a familial housing situation to observe their social development.

10　Until 2011, there was only one castrated gorilla in the GEEP and he is the only recorded

11　castrated individual to have reached adulthood. The reports collected from caretakers reveal

12　that this male had a good quality of life (both in the nursery and in the social group). Given

13　this positive feedback, the GEEP committee recommended the castration of ten immature

14　males living in familial groups between 2007 and 2016, followed by a regular monitoring of

15　their development and careful observation to identify any possible impact on the physical,

16　psychological and behavioural development of these males and of the other members of their

17　familial group.

18　　This study investigates the effect of such castration on immature male gorillas. Social

19　behaviour changes dramatically during primate adolescence, and it is unknown how far

20　adolescent social behavioural development is reliant on testosterone and other gonadal

21　hormones (Richards et al., 2009). In western lowland gorillas, these behavioural and

22　hormonal changes mainly occur during juvenescence (from 3-4 years to 6-7.5 years) and

23　adolescence (from 6-7.5 years to 12-14 years), and continue until they reach adulthood as

24　young silverbacks (from 12-14 years to 18-20 years) (Breuer et al., 2009; Stoinski et al.,

25　2002). It is therefore important to improve our knowledge of how castration effects

1 individuals during these life stages.

2 Zoos do not base their gorilla husbandry decisions in zoos on the physiological and

3 nutritional needs of gorillas alone; they also take the fundamental social needs of this species

4 into account in order to ensure acceptable levels of welfare. We define the socialization

5 process as the acquisition of a social repertoire and the construction of a social network during

6 growth. It is essential to understand the important role that social environment plays in an

7 individual's health and how the management of different social housing situations can

8 improve individual health and welfare (Rose & Croft, 2015; Sueur & Pelé, 2015). These

9 criteria are vital welfare clues to ensure the provision of optimal care and govern the

10 management of surplus males in the captive Gorilla EEP population.

11 More recently, social network analysis (SNA) has been proved to be an efficient tool for

12 the management of zoo animals (McCowan et al., 2008; Sueur et al., 2011), as reviewed by

13 Rose and Croft in 2015, and is increasingly used in this domain. In 2011, a social network

14 analysis of social preferences in a captive chimpanzee community (Clark, 2011) supported the

15 hypothesis that a large and modern exhibit facilitates the expression of social preferences

16 among individuals. The same year, captive chimpanzees with a high social status were shown

17 to occupy central positions in the grooming network (Kanngiesser et al., 2011). This

18 highlighting of the pivotal role played by specific individuals in maintaining cohesiveness

19 could influence how zoos manage the restructuring of groups. The use of SNA may provide

20 valuable information about the different social life stages in intact or castrated immature

21 gorilla males living in familial and bachelor captive social groups.

22 Our study seeks to understand the social differences experienced by castrated and intact

23 individuals living in different social situations - namely familial and bachelor - from the

24 juvenescent to the adolescent maturity phases. Our study hypothesises that these immature

25 captive gorilla males should all show different behavioural types or strategies, depending on

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their social housing and their age. Publications describing captive and wild populations report that intact males emigrated from the familial groups following their gradual peripheralization and a decrease in the number and quality of relationships they had with other group members, particularly the silverback (Abelló et al., 2017; Harcourt, 1978; Harcourt & Stewart, 2007; Harcourt & Stewart, 1977). In contrast, the weaker expected physical development of castrated males on reaching adulthood could facilitate their relationships with younger group members. Maturing intact gorillas that live in bachelor groups instead of living alone could also benefit from the experience of silverbacks (Levréro et al., 2006). We therefore make the following hypotheses: 1) For intact males living in familial groups, positive social interactions will decrease with age; 2) For castrated males living in familial groups, positive social interactions will remain stable or increase; therefore 3) An increase will probably be observed in the number and quality of relationships between castrated immature males and adult conspecifics in familial groups; and finally 4) Significantly more numerous positive social interactions will be observed for intact males living in bachelor groups than for intact males living in familial groups.

Methods

This research project was designed in accordance with the best practices and highest ethical standards, and meets national and international legislation requirements. Moreover, all methods comply with the EAZA Code of Ethics (www.eaza.net) and the WAZA Code of Ethics and Animal Welfare, namely the 'Ethical Guidelines for the Conduct of Research on Animals by Zoos and Aquaria' (www.waza.org).

Subjects and housing

Small sample size is a common cause of difficulty in many studies seeking to carry out long-term monitoring of socialization processes in captive animals (Watters et al, 2009). Our

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1 study addresses this problem through the observation of 93 western lowland gorillas (51

2 males and 42 females) living in eleven different social units (seven familial groups and four

3 bachelor groups) located in nine different zoological institutions; each group was studied for

4 approximately one month (see Table 1 for full details). Individuals between 0-3 years of age

5 were classified as infants (INF), juveniles (JUV) of both sexes were aged between 3-6 years,

6 and adolescents (ADO) were 6-10 years old for females and 6-12 years old for males.

7 Females were considered adults (A) at 10 years of age, and males were considered adults at

8 the age of 18 after a transitory young silverback (YSB) age class from the age of 12 to 18. All

9 the groups had daily access to naturalistic outdoor enclosures or islands measuring between

10 400 and 10 000 square meters in addition to their indoor areas. All the different environments

11 were equipped with appropriate permanent and temporary enrichment for these animals. The

12 housing in all the institutions concerned is accredited under the same Gorilla EEP standards

13 (Abelló et al., 2017, section 2, pages 32 to 51). All of the 10 castrated immature gorillas

14 present in our study were castrated by surgery before the age of three, and a minimum of 6

15 months before the observations began.

16 *Data collection*

17 BL collected all data for each group over approximately one month between April 2016

18 and May 2017 (see Table 1). Observations were carried out from 9:00 a.m. to 5:00 p.m, when

19 some of the groups observed solely had access to their outside enclosure and the others were

20 free to move between the inside and outside enclosures according to group management and

21 weather conditions. Individuals in the infant age class (0-3 years old) were not included in

22 observation data because they were still dependent on their mothers.

23 We defined "social preference proximity" as a spatial association within one meter of the

24 focal individual, with or without contact, and the "social tolerance proximity" as distances of

25 one to five meters between the focal individual and a conspecific. The sum of social

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1   preference and tolerance proximities provides the "general social proximity" spatial

2   associations (within five meters of the focal individual).

3   Depending on the number of individuals per group, observations were made using two to

4   four 10-minute continuous focal animal samplings per day for each group member. We

5   recorded proximities between individuals but excluded those relating to aggressions, thus

6   retaining proximities that occurred during affiliative or neutral behaviours (see Table S1) in

7   order to solely interpret data that are collected in a context of "positive" welfare and

8   comparable for all groups. When a focal individual was in the proximity of more than one

9   conspecific, the observer recorded the number of individuals and the exact duration whenever

10 the perimeters of each individual changed (from social preference proximity to social

11 tolerance proximity, within a 5 meter radius of the focal individual). Samplings were

12 randomized throughout the day and thirty 10-min focal samplings (i.e. a total of five hours)

13 had been obtained per individual by the end of the observations.

14   In parallel, instantaneous samplings were collected every 15 minutes and provided

15 information on "positive" proximity patterns (using the same ethogram detailed in

16 Supplementary Material, Table S1). The scan was valid if, and only if, all the group members

17 were seen within one minute of beginning the scan sampling. Approximately 20 scans were

18 carried out per day to obtain 200 scans per group.

19   Proximity data were discarded from the dataset when aggressive behaviours were

20 recorded, to ensure that we only measured proximities as a proxy of affiliative relationships

21 (stability indicator). We decided to concentrate our analyses solely on a positive pattern of

22 proximities as a "positive index of welfare" because aggressive behaviours are rare in both

23 wild and captive environment (Nakamichi & Kato, 2001; Stokes, 2004). Moreover, additional

24 data collection for aggressive behaviours would have required all occurrences samplings,

25 which was not achievable with a single observer. The data collected from focal animal

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1   samplings (in terms of durations), and from the instantaneous samplings (in terms of

2   occurrences) were used to build proximity matrices of the "positive" patterns performed at

3   social preference, social tolerance, then finally general social proximities for each group (see

4   next paragraph).

5   *Social network analysis*

6   Social network analysis (SNA) required the collection of all dyadic proximity patterns in

7   a studied group. Observation matrices (at social preference, tolerance, and general proximity)

8   were built by considering the quotient recorded during the observations for each of the two

9   individuals, thus obtaining an average dyadic social proximity value. The sociality focal and

10   scan matrices for each group were compared using Dietz' R matrix correlation tests (1 000

11   permutations in SOCPROG 2.8, see Supplementary Material, Table S2). The average R-

12   correlation coefficients of the 11 groups were R=0.89, R=0.82, and R=0.77 for general social

13   proximity, social preference proximity and social tolerance proximity, respectively, and were

14   highly correlated (combined P-value < 0.0001; R-package CombinePValue). These

15   correlations confirm the validity of all data collected and the use of both matrices (built after

16   focal and scan observations) in the same way for the statistical analysis.

17   The indices of the matrices of associations were obtained with SOCPROG 2.8

18   software (Whitehead, 2009). The weighted networks of familial and bachelor groups are

19   represented as graphs via Gephi software (https://gephi.github.io) (see Supplementary

20   Material, Figures S1 to S10). We focused on the strength index for an individual, which is

21   equal to the sum of the total duration/occurrence of proximities with all group peers in our

22   study. Individuals with a high strength index have strong associations with others and/or have

23   many associates (Carter et al., 2013). By dividing the strength index of a chosen individual by

24   the number of group partners, we obtained what we called a personal sociality index (PSI).

25   This index thus determines both the activity budget time and social affinities by revealing

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"what the individual wants to do near which conspecifics". It is therefore an individual indicator of cohesion.

Statistical Analyses

Analyses were performed to compare 27 JUV and ADO males. Amongst these males, 9 intact ADO males lived in bachelor groups and the remaining eighteen males lived in familial groups: nine were castrated (5 JUV and 4 ADO) and nine were intact (5 JUV and 4 ADO) - see details of immature males in Table 2. The data for Mapenzi (castrated ADO in the Beauval group) and Nakouh (intact ADO in the Burgers zoo group) were excluded from all tests after being identified as outlier values on the boxplot distribution for a number of variables (see Figure S11 in Supplementary Material, and further details in the Discussion section). We used tests to look for differences as a function of age classes, fertility status (castrated vs. intact), and housing situation (familial or bachelor groups) for the following variables: (1) PSI, (2) percentage of time spent in isolation (no conspecifics within a 5 meter radius), (3) percentage of time spent in social play behaviours, (4) percentage of time spent in social proximity with the silverback, (5) percentage of time spent in social proximity with the mother, and (6) percentage of time spent in social proximity with adult females. Both social preference and tolerance proximities were taken into account when testing the variables for PSI and the percentage of time spent in proximity with the adult peers. We ran our analyses in three steps:

- Comparing variables with age.

First, Spearman rank correlation tests with permutations (Spearman test function in the R coin package) were conducted to establish the "positive" social patterns of the captive immature males through determined functions (fertility status and housing situation).

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1   • Comparing variables specifically for adolescents.

2 In a second step, one-way analysis with permutation tests (perm.oneway.anova in the R-

3 package wPerm) and pairwise permutation post-hoc tests were performed to compare the

4 mean as a percentage of time for the three categories of ADO males for variables 1 to 3 (intact

5 males living in bachelor groups, intact and castrated males living in familial groups).

6   • Comparing variables specifically for immature males living in familial groups.

7 In a last step, permutation tests for independent samples (permTS in the R package perm)

8 were performed to look for any significant differences among the castrated and intact

9 immature males living in familial groups (variables (1) to (6) for the JUV age class, and

10 variables (4) to (6) for the ADO age class). Despite our small sample size, we decided to

11 exclude the data of the two outliers given that the high number of permutations strengthened

12 the results of our tests.

13 All the analyses run in R (version 3.4.2) were two-tailed and the probability of a type I error

14 was maintained at 0.05. All tests were performed with 9999 permutations.

15 **Results**

16   Matrices of scan associations were analysed to obtain the sociograms of the 11 groups

17 (Figure 1: Artis group example, see Supplementary Material for the other groups, Figures S1

18 to S10).

19   *1) Personal social index (PSI)*

20 The evolution of the personal social index PSI was compared to age for the three categories of

21 males using Spearman rank correlation tests with permutations. A negative correlation was

22 noted for intact males living in familial groups at social preference proximity (Fig. 2A) (rho=-

1 0.95, P=0.007) and at social tolerance proximity (Fig 2B) (rho=-0.88, P=0.015). No

2 correlation was found for castrated males living in familial groups at social preference

3 proximity (rho=-0.37, P=0.3), whereas a positive correlation was observed at social tolerance

4 proximity (rho=0.72, P= 0.043). No correlations were observed for the intact males living in

5 bachelor groups at both social preference (rho=0.13, P=0.704) and social tolerance proximity

6 (rho=0.19, P=0.586). Permutation tests in the two JUV categories (intact and castrated) living

7 in familial groups did not reveal any significant differences at social preference (P=0.373) or

8 social tolerance proximity (P=0.984). One-way analysis of the three ADO categories of

9 immature males did not reveal any significant differences at social preference proximity, with

10 a value of P=0.207. However, a trend of significant difference (P=0.085) was observed at

11 social tolerance proximity. Pairwise permutation tests revealed that the PSI at social tolerance

12 proximity for castrated ADO individuals living in familial groups was significantly higher

13 than that of intact ADO males living in the same context (P_{adjust}=0.032). The other pairwise

14 comparisons reveal no differences (intact in familial groups – intact in bachelor groups:

15 P_{adjust}=0.636; castrated in familial groups – intact in bachelor groups: P_{adjust}=0.128).

16   *2) Isolation time*

17 Spearman rank correlation testing between the percentage of time budget spent in isolation

18 and the age of individuals indicated a positive correlation (rho=0.90, P=0.011) for intact

19 males living in familial groups (see FIG 3A). There were no correlations for castrated males

20 living in familial groups (rho=0.13, P=0.706) and for intact males living in bachelor groups

21 (rho=0.10, P=0.776). Permutation tests for the two JUV categories living in familial groups

22 did not reveal any significant differences in mean values for isolation (P=0.249). One-way

23 analysis for the three ADO categories of immatures males for the percentage of time spent

24 alone revealed significant differences (P<0.001), with significantly less isolation in ADO

25 castrated males (mean=15.15%±2.68) than in both intact ADO males living in familial groups

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1 (mean=30.61%±3.8) (P_{adjust}=0.033) and intact ADO males living in bachelor groups

2 (mean=50.95%±6.08) (P_{adjus}t=0.009). Intact ADO males living in bachelor groups were also

3 more isolated than intact males living in familial groups (P_{adjust}=0.029).

4   *3) Social play*

5 Spearman rank correlation testing between the percentage of time budget spent in social play

6 and the age of individuals (see FIG 3B) revealed a trend of negative correlation for intact

7 males living in bachelor groups (rho=-0.64, P=0.072) and for intact males living in familial

8 groups (rho=-0.60, P=0.08). However, no correlation was found for castrated males living in

9 familial groups (rho=-0.18, P=0.604). Permutation tests for the two JUV categories living in

10 familial groups did not reveal any significant differences in mean values for social play

11 (P=0.786). One-way analysis of the percentage of time budget spent in social play highlighted

12 significant differences between the three ADO categories of immatures males (P=0.016).

13 Post-hoc pairwise comparisons showed that castrated ADO males living in familial groups

14 tended to be significantly more involved in social play than intact ADO males living in

15 bachelor groups (Padjust=0.056), whereas no differences were found for the other pairwise

16 comparisons (intact ADO males in familial groups - intact ADO males in bachelor groups:

17 P_{adjust}=0.965; intact ADO males in familial groups - castrated ADO males in familial groups:

18 P_{adjust}=0.118). However, complementary permutation tests comparing the amount of social

19 play by males during juvenescence and adolescence highlighted that intact adolescents were

20 significantly less involved in play than intact juveniles (P=0.015), contrary to observations in

21 castrated immature males (P=0.73).

22   *4) "Positive" pattern of proximity with the silverback proximity*

23   The following results concern social variables that are only present in the familial

24 housing situation, and highlight the differences between the two fertility statuses (intact vs.

14

1 castrated). Figure 4 compares the percentage of budget time used to perform positive

2 behaviour in the proximity of the silverback. The Spearman rank tests revealed a negative

3 correlation between age and the percentage of proximity with the silverback at social

4 preference proximity (Fig. 4A, rho=-0.85, P=0.017) and at social tolerance proximity (Fig.

5 4B, rho=-0.95, P=0.008) for the intact males. However, no correlations were found for the

6 castrated males at social preference proximity (Fig. 4A, rho=-0.15, P=0.666) or at social

7 tolerance proximity (Fig. 4B, rho=-0.32, P=0.370). Permutation tests comparing associated

8 means revealed that castrated ADO males performed significantly more positive behaviours at

9 social tolerance proximity with the silverback than the intact ADO males did (P=0.027). No

10 differences were found for the JUV and ADO males at social preference proximity (for JUV

11 P=0.421; for ADO P=0.543), or for the JUV males at social tolerance proximity (P=0.857).

12 *5) "Positive" pattern of proximity with the mother*

13 As some individuals did not have their mother in their group, it is important to note that

14 the sample size is smaller than the initial one for the tests on this variable (N=8 for intact

15 males (5 JUV + 3 ADO); N=7 for castrated males (4 JUV + 3 ADO)). For both categories

16 (intact and castrated), Spearman rank correlation tests revealed negative correlations at social

17 preference proximity when juveniles males were compared to older adolescents (FIG 5A,

18 intact: rho=-0.98, P=0.009; castrated: rho=-0.89, P=0.029). No correlations were found for the

19 same test at social tolerance proximity (FIG 5B, intact: rho=-0.57, P=0.120; castrated:

20 rho=0.29, P=0.484). The comparisons of associated means did not reveal any differences

21 between the two categories of males for JUV and ADO age classes (permutation tests at social

22 preference proximity for JUV P=0.413 and for ADO P=0.5; and at tolerance proximity for

23 JUV P=0.111and for ADO P=0.3).

24 *6) "Positive" pattern of proximity with the adult females*

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A ratio was used to allow comparisons between different numbers of females in each group. Spearman rank correlation tests did not reveal any correlation at social preference proximity when intact juveniles males were compared to older intact adolescents, and a trend of significant positive correlation was observed for castrated males (FIG 6A, intact: rho=0.10, P=0.813; castrated: rho=0.68, P=0.053). A positive correlation was observed for castrated males at social tolerance proximity, whereas positive behaviours in the proximity of adult females decreased with age for intact males (FIG 6B, intact: rho=-0.53, P=0.136; castrated: rho=0.82, P=0.019). The permutation tests did not reveal any significant differences at social preference proximity (for JUV P=0.532 and ADO P=0.257). Likewise, no difference was observed for the JUV age-class (P=0.571) at social tolerance proximity. However, castrated ADO males performed significantly more positive behaviours towards adult females than the intact ADO males did (P=0.029).

Discussion

This is the first study to focus on the socialization process of immature male gorillas in captivity, according to both the fertility status (castrated or intact) and the social composition (familial or bachelor grouping). These comparisons between the three categories of immature males, i.e. intact and castrated living in a familial group; and intact living in a bachelor group, revealed significant differences according to the personal sociality index, the percentage of time budget spent in isolation, and the percentage of time budget spent on social play.

The first finding is that the differences between the male categories from different age classes only occurred within social tolerance proximity (between one to five meters). It was not surprising that no differences were observed at social preference proximity (within one metre of the focal contact) because unlike chimpanzees and bonobos, gorillas generally perform few positive behaviours in the close proximity of a conspecific, as mentioned in a number of studies (Chelluri et al, 2013; Furuichi & Ihobe, 1994). Secondly, in accordance

16

1   with the history life trait already described for gorilla species, intact males living in familial

2   groups became less and less socially cohesive as they grew up (i.e. the personal sociality

3   index decreased significantly at both social preference and tolerance proximity). Our results

4   converged with those stating that spatial associations, proximity and affiliation decrease as the

5   frequency and intensity of aggression increases in both wild (Harcourt & Stewart, 1981;

6   Robbins et al., 2004; Watts & Pusey, 1993) and captive environments (Abelló et al., 2017;

7   Stoinski et al, 2004; Vermeer et al., 2014). This generates a progressive peripheralization until

8   the emigration (in the wild) or the transfer (human management in captivity) of the male from

9   the natal group. Additionally, maturation during adolescence is accompanied by intense

10 morphological changes in stature: maturing males increasingly differ from their younger

11 conspecifics in terms of body size and social skills. This leads to unbalanced power relations

12 which explain the increased spatial distance with the other immature members of the group,

13 and, in turn, a lower intragroup cohesiveness (i.e. a decrease in the sociality index for the

14 adolescence age class). Immature males housed in bachelor groups contrasted with those

15 housed in familial groups because their sociality index did not evolve significantly during

16 adolescence. Wild male mountain gorillas have been reported to live together for years in

17 unisex groups if they are not joined by females (Fossey, 1983; Yamagiwa, 1987a, 1987b).

18 Multimale groups are rare in western lowland gorillas (Magliocca et al, 1999; Parnell, 2002),

19 but an all-male structure was observed for long periods of between 13 months and 3 years in

20 observed groups that contained more than one immature or adult male (Gatti et al, 2004;

21 Robbins et al., 2004). Levrero and colleagues also reported wild western lowland gorilla

22 bachelor groups in 2006, but none of these groups were composed of several silverbacks.

23 Furthermore, strong affiliative relationships among males in a captive bachelor group are

24 most likely to occur when males are immature (Stoinski et al., 2004). It is therefore preferable

25 to transfer immature males at an early age if they are destined for life in a bachelor group,

17

1 because socialization with other males is easier with younger animals (Abelló et al., 2017).

2 These different aspects, as well as the absence of competition for mating in captive bachelor

3 groups, could explain the stability of the sociality index for the adolescent bachelor males

4 studied. With the exception of the differences highlighted between the two housing situations

5 (familial and bachelor grouping), our results underline contrary types of social changes

6 according to the fertility status of individuals. Comparison of juvenescent and adolescent life

7 stages showed that while intact males are excluded from the familial group at adolescence,

8 castrated males significantly increased their intragroup cohesiveness at tolerance. Moreover,

9 analyses in the familial groups revealed significantly more cohesion in social bonds for

10 castrated adolescents compared to intact males of the same age class.

11 The results for isolation time are in concordance with our findings on the personal

12 sociality index. The intact adolescent males living in a familial group were significantly more

13 isolated than the castrated adolescent males, and, the intact adolescent males living in a

14 bachelor group spent significantly more time in isolation than both intact and castrated

15 adolescent males living in a familial group. Like in the wild, the "positive" or "negative"

16 reactions between males in a captive bachelor group are expected to be directly related to the

17 perceived affinity with a conspecific, but also to a possible threat of a specific male, reflecting

18 both the degree of vulnerability of the latter (his age and physical condition) and his relative

19 familiarity with the other males. Consequently, zoos that are designing an enclosure for a

20 bachelor group are advised to follow the recommendations made by Stoinski et al., in 2004(b)

21 and Coe et al. in 2009 to ensure that gorilla males can control how much space they are able

22 to put between themselves and conspecifics. Young silverback individuals were present in

23 two of the bachelor groups studied (Amneville group 2 and Loro Parque), and this factor

24 could explain the higher isolation rates observed for intact adolescent males in a bachelor

25 group. Also, time spent in isolation may simply be the expression of the individual's personal

18

1 desire to be alone. Similarly, the captive housing conditions of a familial group should be

2 carefully considered when anticipating the removal of intact males that have reached the end

3 of adolescence, due to the possible increase in conflicts with the silverback (personal

4 observations). Maturing intact adolescents tend to challenge their fathers (and conversely),

5 and this can cause social stress for all group members. The housing should provide enough

6 space for gorillas to avoid these conflicts, and be complex enough to provide safe escape

7 routes and isolation areas. In this respect, the different management strategies evaluated in

8 this study (familial and bachelor grouping) can permit individuals to avoid conflict, and thus

9 become a critical a reliable tool to improve the well-being of social species maintained in

10 captivity (Morgan & Tromborg, 2007). Given that the significantly higher share of isolation in

11 the time budget of intact males living in bachelor groups does not impact the personal

12 sociality index (i.e. there are no differences between intact males living in the different

13 housing situations), it is likely that male-male interactions are promoted in the unisex social

14 context. These findings suggest that gorillas have the possibility to selectively modify the

15 distribution of some typical patterns of their behavioural repertoire according to the housing

16 situation and the social composition of the group. This high level of behavioural flexibility

17 has been also highlighted in captivity by testing the crowding effect in the Apenheul gorilla

18 group (Cordoni & Palagi, 2007). The dynamic of the social networks emerging from social

19 relationships between members and the pattern of activity time budget are constantly

20 evolving, and therefore require a detailed follow-up to ensure optimal captivity welfare. Our

21 study protocol highlights that social network analysis is a useful tool to improve the

22 monitoring of the different management strategies used for animals in captivity.

23 Results for the involvement of the immature males in social play are in concordance with

24 the known life history traits for gorilla species. Whatever the housing situation, all intact

25 males tended to play significantly less from juvenility to adolescence, and even during

19

adolescence. This evolution is due to changes in time budgets during maturation (increased

foraging time as well as a growing interest in other social activities such as agonism and sex),

leading to an overall decline in play at the end of the juvenile period. Moreover, as for other

primate species such as the chimpanzee (Shimada & Sueur, 2014) and Japanese macaques

(Shimada & Sueur, 2018), it appears that social play mainly fulfils the function of

strengthening social bonds during juvenility, with a significant decrease during adolescence.

The results of Maestripieri and Ross' study in 2004 were consistent with both motor training

and social skills hypotheses for captive gorillas aged from 0 to 5 years. Our results and those

of Maestripieri and Ross (2004) highlight the importance of considering "social

compatibilities" during the formation of bachelor groups. Like other primate species,

immature gorillas are expected to play and interact mostly with individuals that have

equivalent body size and social skills (Fagen, 1981; Fairbanks, 1993). This morphological

compatibility factor is a major concern for the formation and maintaining of all-male groups

in captivity. The absence of appropriate social partners is the major factor that could explain

the outlier data recorded for the castrated individual Mapenzi, housed in a familial group at

Beauval zoo (see Supplementary Material, Fig. S11). The same may apply to the outlier data

for Nakouh, an adolescent intact male in Burgers' zoo (see Supplementary Material, Fig.

S11). An adult female from this institution gave birth on the 13th June 2013 to twins, N'kato

and N'hasa. This event is very rare in gorillas and may explain the data recorded for Nakouh:

the presence of a new-born in a group induces a significant reduction in inter-individual

distance not only for characterized specific dyadic interactions (Nakamichi & Kato, 2001;

Stoinski et al, 2003) but also for general group cohesion (Kurtycz et al, 2014). Moreover,

there were no older immature conspecifics with whom Nakouh could interact. He did live

with three younger males during his socialization process. Nakouh's socialization process

may have been delayed by this social imbalance. However, complementary tests comparing

20

the share of social play between juvenile and adolescent age classes underline that castrated individuals do not decrease their involvement in social play during these two life stages, unlike the intact males. The combined results on the three variables described (personal sociality index, isolation and share of social play in time budget) highlight that captive western lowland gorillas are socially flexible, and confirm that maturing males adapt well to the bachelor management strategy that has been implemented for over three decades. Indeed, the "positive" interactions prioritised by males maintain social cohesion despite a greater share of isolation in the activity budget time, suggesting that maturing males are adapting well to bachelor group housing. Finally, the different behavioural patterns presented in our study suggest that castration has a positive impact on the intra-group cohesiveness of the individuals during juvenescence and adolescence.

While gorilla familial groups are mainly based on adult male-female bonds (Harcourt & Stewart, 2007), relationships between the silverback and its offspring play a significant role in group structure. As already shown in different studies, the close bonds between the adult male and the immature males (Rosenbaum et al, 2016; Stewart, 2001; Yamagiwa, 1983) are best explained as paternal care (protection and tolerance of proximity) rather than a significant investment in their offspring (resting in contact, grooming, play) (Rosenbaum et al, 2011). The "positive" behaviours that intact immature males performed at preference proximity of the silverback and the mother decreased significantly when they reached maturity. This was also the case at tolerance proximity with the silverback. Conversely, in accordance with our results on the personal sociality index, castrated males keep strong social bonds with the silverback and the adult females when they reach adolescence life stage (i.e. a significant increase at tolerance proximity during maturation). This increase in proximity and interactions might be explained by the fact that conspecifics perceive changes induced by castration that could be visual, auditory, olfactory, and/or behavioural (Caillaud et al., 2008; Masi & Bouret,

1 2015). Our study therefore highlights not only behavioural changes for castrated individuals,

2 but also a different perception of the latter by their group peers. Although our study did not

3 address this issue, our results suggest an effect of castration on the development of social

4 bonds. The castration induces a cancellation of the growth associated with the first stage of

5 androgen increase during adolescence (Stoinski et al., 2002) (see Supplementary Material,

6 Fig. S12), and could for example increase "the social compatibilities" between the

7 developmentally staggered individuals that compose the group. The behavioural and

8 morphological modifications observed may improve group cohesiveness, in accordance with

9 the social and motor skills hypotheses (Baldwin & Baldwin, 1974; Byers, 1998).

10 As physical, social or psychological alterations are often associated with subtle changes

11 in behaviour, our behavioural monitoring data can be beneficial to many areas of gorilla

12 husbandry. The collaboration of European zoos in this study has ensured a low number of

13 biases due to care routines, diet recommendations and environmental standards that all follow

14 the same set of guidelines recommended by the EEP (for details see Abelló et al., 2017). We

15 acknowledge that caution must be taken when making our conclusions, as the individuals

16 involved were observed for just one month of their development. For this reason, future

17 research should be carried out over the long-term to gain a more detailed knowledge of the

18 social and physiological development of castrated males in familial groups and intact males in

19 bachelor groups.

20 **Conclusion and perspectives**

21 Our study suggests that the housing of castrated surplus males in familial groups is a

22 feasible alternative strategy for positive socio-behavioural management during the maturation

23 of gorilla males. Indeed, our results highlight that castrated adolescents are significantly more

24 cohesive in their native group than their intact counterparts. Furthermore, our results

25 comparing intact immature males living in familial and bachelor contexts are in concordance

22

1 with those of all the previous studies focusing on captive gorilla bachelor groups. These

2 results strengthen the efforts made by the Gorilla Eaza Ex-situ Programme (GEEP) to

3 improve the different housing management strategies designed to solve the growing problem

4 of surplus male gorillas in captivity. We recommend avoiding the castration of immature

5 males that have no other immature male peers in their group (as seen in the case of Mapenzi, a

6 castrated adolescent male excluded as outlier data from our analyses). Immature males that

7 are transferred into bachelor groups should be pair-generational individuals that share the

8 same developmentally staggered stages, as described by the motor-training hypothesis and the

9 social-relationship hypothesis of play (Maestripieri & Ross, 2004) and social development in

10 general (this study). Other factors such as enclosure size, differences in facility design

11 features, effects of spatial crowding, group size and daily care routine could all affect the

12 proximity between gorillas group members and their behaviour (Coe et al., 2009; Kuhar,

13 2008; Ross, Calcutt, Schapiro, & Hau, 2011). It is unlikely that all of these factors explain all

14 of the variation in social dynamics, it will nevertheless be essential to include these covariates

15 in the next studies. Moreover, future studies are necessary to investigate whether castrated

16 males have behavioural similarities with females, and understanding how castration

17 influences physical and hormonal development can help us to better understand the long-term

18 effects of this contraceptive method on the social dynamics of the group. Our results should

19 be complemented with a further study comparing the networks of "negative" proximity

20 pattern in the same way as we did here for "positive" proximity. Finally, the long-term

21 monitoring of castrated males is necessary, especially from the young silverback age-class

22 until adulthood, to ascertain whether the use of castration as an additional socio-behavioural

23 management strategy is consistent over time and meets the welfare criteria for maintaining

24 this species in captivity.

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20   **Table legends**

21   Table 1: Composition details of the familial and bachelor groups observed. FSC= familial

22   social context; BSC= bachelor social context. The two grey columns highlight the subjects for

23   whom data are retained for analysis and interpretation in this study (detailed in Table 2)

Institutions	Type of group	period of observation (month/year)	Number of animals	Adults (A)	Young Silverback (YSB)	Adolescent (ADO) [Intact/Castrated]	Juveniles (JUV) [Intact/Castrated]	Infants (INF)

32

				♂ >18y	♀ >10y	♂ 12-18y	♂ 6-12y	♀ 6-10y	♂ 3-6y	♀ 3-6y	♂ <3y	♀ <3y
Artis	FSC	04/2016	10	1	3	0	2 [2/0]	0	3 [2/1]	0	1	0
Apenheul	FSC	07/2016	14	1	5	0	2 [2/0]	1	2 [1/1]	3	0	0
Beauval	FSC	05/2016	13	1	4	0	1 [0/1]	2	0	3	2	0
Burgers'zoo	FSC	08/2016	12	1	4	0	1 [1/0]	1	2 [2/0]	1	1	1
Chessington	FSC	09/2016	8	1	4	0	1 [0/1]	0	1 [0/1]	1	0	0
Gaïazoo	FSC	06/2016	9	1	3	0	2 [0/2]	0	1 [0/1]	0	1	1
La Vallée des Singes	FSC	09/2016	9	1	4	0	1 [0/1]	0	1 [0/1]	1	1	0
Amneville group 1 (G1)	BSC	04/2017	3	1	-	0	2	-	-	-	-	-
Amneville group 2 (G2)	BSC	04/2017	5	1	-	2	2	-	-	-	-	-
Beauval	BSC	05/2016	5	1	-	0	4	-	-	-	-	-
Loro parque	BSC	03/2017	5	3	-	1	1	-	-	-	-	-
Total	-	10 months	93	13	27	3	19 [14/5]	4	10 [5/5]	9	6	2

1

2 Table 2: Details concerning the immature males studied in FSC (familial groups) and BSC

3 (bachelor groups). Among the 29 subjects, the two grey individuals were excluded as outliers.

Name of the individual	Institution	Sexual status	Birth	Social context	Age during observation (years)	Age class
N'KATO	Burgers'zoo	intact	13/06/2013	FSC	3.2	Juveniles (JUV)
NUKTA	Burgers'zoo	intact	25/03/2013	FSC	3.4	
AYO	Gaïazoo	intact	31/12/2012	FSC	3.5	
DOULI	Artis	intact	27/02/2012	FSC	4.1	
MZUNGU	Apenheul	intact	26/06/2011	FSC	5.1	
NAKOUH	Burgers'zoo	intact	04/11/2009	FSC	6.9	Adolescents (ADO)
DAYO	Artis	intact	18/06/2008	FSC	7.9	
WIMBE	Apenheul	intact	12/04/2008	FSC	8.3	
MAPASA	Apenheul	intact	15/10/2007	FSC	8.8	
SHOMARI	Artis	intact	12/07/2007	FSC	8.8	
KAJOLU	Beauval	intact	08/12/2009	BSC	6.5	
UPALA	Amneville G2	intact	27/05/2008	BSC	9.0	
UBONGO	Loro parque	intact	06/01/2008	BSC	9.3	
BANJOKO	Beauval	intact	16/12/2006	BSC	9.5	
SADIKI	Beauval	intact	10/10/2006	BSC	9.7	
MONZA	Amneville G2	intact	02/09/2007	BSC	9.7	
AKIKI	Amneville G1	intact	04/04/2007	BSC	10.2	
N'GORO	Amneville G1	intact	25/08/2006	BSC	10.8	
KUMI	Beauval	intact	20/08/2004	BSC	11.9	
JABARI	Apenheul	castrated	22/12/2012	FSC	3.6	Juveniles (JUV)
SHAMBE	Artis	castrated	04/09/2011	FSC	4.6	
MWANA	Chessington	castrated	23/02/2012	FSC	4.6	
BEMBOSI	Artis	castrated	31/05/2011	FSC	4.9	
MAWETE	La Vallée des Singes	castrated	20/11/2011	FSC	5.0	
MAPENZI	Beauval	castrated	14/04/2010	FSC	6.2	Adolescents (ADO)
MOSI	Gaïazoo	castrated	10/02/2010	FSC	6.4	

MBULA	Chessington	castrated	10/03/2009	FSC	7.6	
MBULA	Chessington	castrated	10/03/2009	FSC	7.6	
DJOMO	La Vallée des Singes	castrated	16/09/2008	FSC	8.2	
LOANGO	Gaïazoo	castrated	23/12/2004	FSC	11.6	

Figure legends

Fig 1: Weighted graphs of positive sociality scan network for the Artis group at (A) GSP (social general proximity), (B) SPP (social preference proximity), and (C) STP (social tolerance proximity). A specific size is assigned for each node (representing one individual). This size is derived from the entry in the social proximity matrices indicating the strength of the social bonds (the frequency of positive behaviours performed at GSP, SPP, or STP proximity within all dyads) (Kasper & Voelkl, 2009). On these circular representations, node sizes are ordered by ascending order of strength index. The thickness of the links between two nodes represents the amount of positive social interactions recorded. The age class of each individual, i.e. adult (A), adolescent (ADO), juvenile (JUV), and infant (INF), is indicated after the name of the individual in the circle. The colours inside the circles represent the sex of the individual: white for females, dark grey for males, and light grey for castrated males.

Fig 2: Changes in strength ratio (=PSI, variable 1) with age for the three categories of immature male (intact and castrated males living in familial group (FSC), and intact males living in bachelor groups (BSC) at (A) social preference proximity (SPP) and (B) social tolerance proximity (STP). LTC indicates linear trend curve.

Fig 3: Changes in percentage of time budget spent in isolation (variable 2, 3A) with age for the three categories of immature males (intact and castrated males living in familial groups (FSC) and intact males living in bachelor groups (BSC)) and changes in the percentage of time budget dedicated to social play with age for the same individuals (variable 3, 3B). LTC indicates linear trend curve.

Fig 4: Changes in percentage of time budget spent in proximity with the silverback with age

34

1   for the immature males (intact and castrated) (variable 4) living in familial groups (FSC), at

2   social preference proximity (SPP) (4A) and at social tolerance proximity (STP) (4B). LTC

3   indicates linear trend curve.

4   **Fig 5**: Changes in percentage of time budget spent in proximity with the mother (variable 5)

5   with age for immature males (intact and castrated) living in familial groups (FSC), at social

6   preference proximity (SPP) (5A) and at social tolerance proximity (STP) (5B). LTC indicates

7   linear trend curve.

8   **Fig 6**: Changes in percentage of time budget spent in proximity with adult females (variable

9   6) with age for immature males (intact and castrated) living in familial groups (FSC) at social

10   preference proximity (SPP) (6A) and at social tolerance proximity (STP) (6B). LTC indicates

11   linear trend curve.

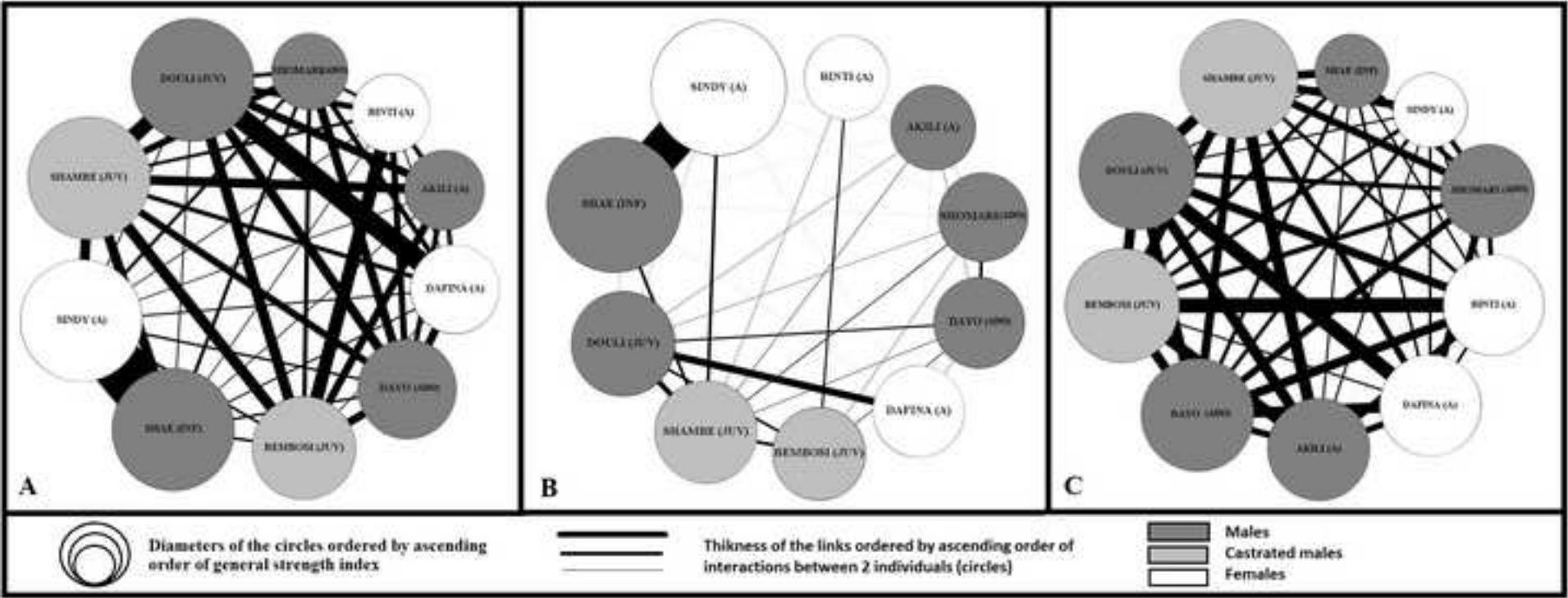**Figure 1**
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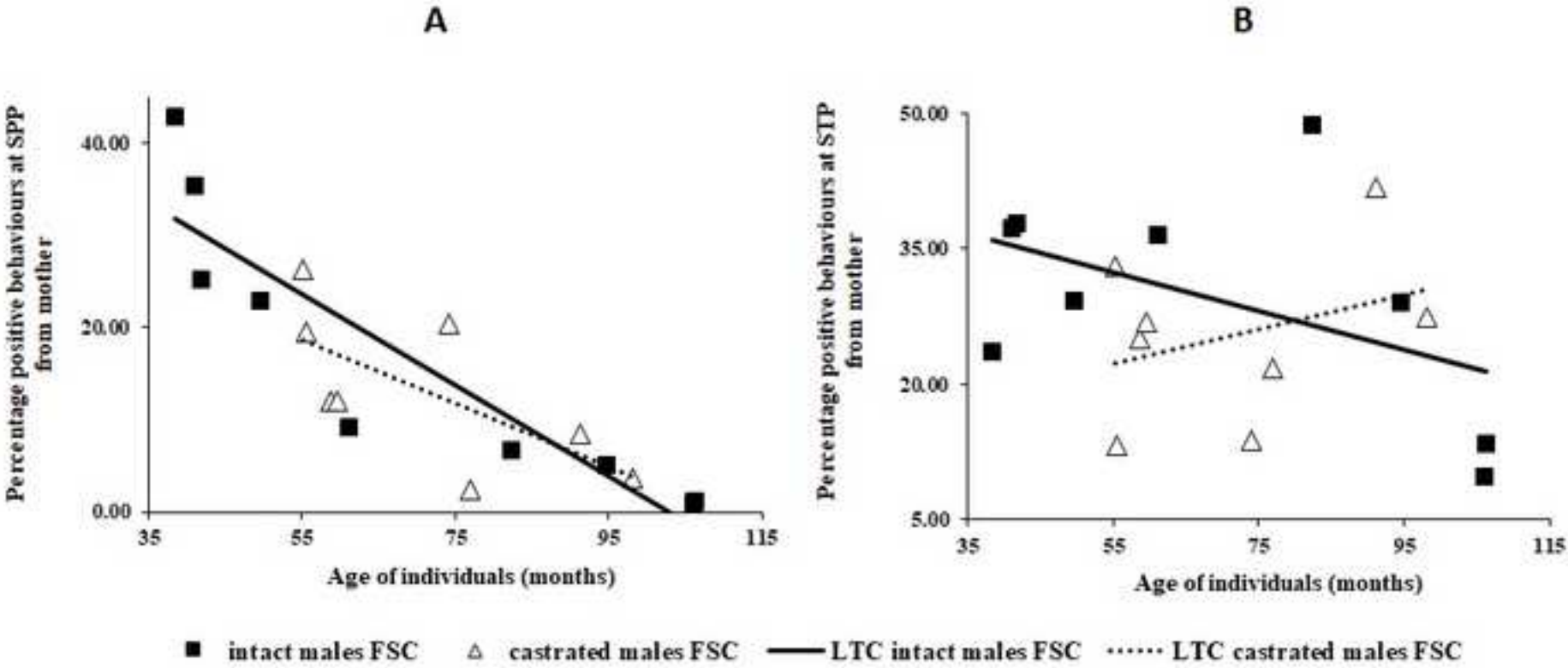Figure 2
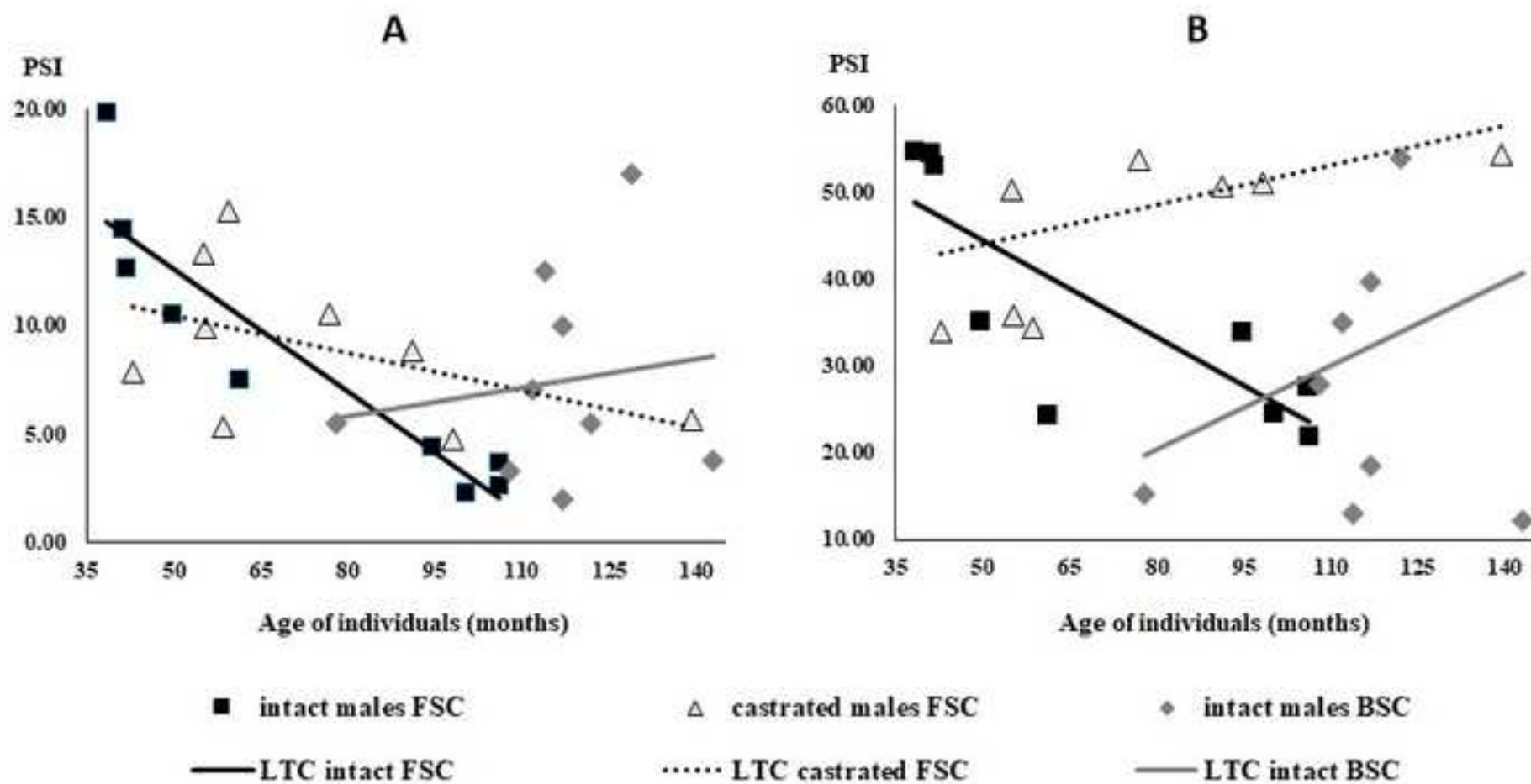
Figure 3
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Figure 3

Figure 4

A

B

Percentage positive behaviours at SPP from mother

Percentage positive behaviours at STP from mother

Age of individuals (months)

Age of individuals (months)

■ intact males FSC   △ castrated males FSC   —— LTC intact males FSC   ······ LTC castrated males FSC

A

B

Ratio of positive behaviours at SPP from the adult females

Ratio of positive behaviours at STP from the adult females

Age of individuals (months)

Age of individuals (months)

■ intact males FSC   △ castrated males FSC   —— LTC intact males FSC   ······ LTC castrated males FSC