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Structural comparison of stress behavior in human's two closest living primate relatives, chimpanzees (*Pan troglodytes*) and bonobos (*Pan paniscus*)

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ABSTRACT

Structural comparison of stress behavior in human's two closest living primate relatives, chimpanzees (*Pan troglodytes*) and bonobos (*Pan paniscus*)

Barnich Rose, 2023 – 2024

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Supervisors: Nicky Staes and Fany Brotcorne

Despite their close genetic relationship, chimpanzees (*Pan troglodytes*) bonobos (*Pan paniscus*) exhibit significant differences in their socio-behavioral patterns. We can wonder if these might be reflected in their response to stress. However, observational studies comparing rates of stress in the two species are lacking and therefore limiting our understanding of what influences stress in chimpanzees and bonobos. Here we used focal and all occurrences behavioral observations to quantify and qualify the rates of four displacement behaviors – rough autoscratching, gentle autoscratching, yawning and nose wiping – that are known for being stress-related behaviors in primates. We observed that despite what was expected, bonobos and chimpanzees do not differ in their rates of displacement behaviors (with the exception of yawning) and that differences are actually higher when comparing within-species groups. Since correlations between the four displacement behaviors were low—except for the correlation between rough and gentle autoscratching in chimpanzees—it suggests that stress may be perceived in varied ways and can reflect different levels of arousal. Individual factors, such as sex, age, and aggression received influence displacement behaviors in chimpanzees and bonobos. Female chimpanzees were found to engage in higher levels of both rough and gentle autoscratching compared to males, while male bonobos exhibited more gentle autoscratching than females, reflecting the species-specific social structures. Older individuals showed fewer displacement behaviors, suggesting improved stress regulation with age. Interestingly, aggression received was linked to a decrease in gentle autoscratching, underscoring the role of context in interpreting displacement behaviors. These findings underscore the need for a broader approach when studying displacement activities in the future.

RESUME

Comparaison structurelle des comportements liés au stress chez les deux espèces les plus proches de l'être humain, les chimpanzés (*Pan troglodytes*) et les bonobos (*Pan paniscus*).

Barnich Rose, 2023 – 2024

UAnvers : Centre pour la recherche et la conservation (CRC) du zoo d'Anvers et du zoo de Planckendael – Nicky Staes

ULiège : Département de Biologie, Ecologie et Evolution – Unité de Biologie du Comportement – Fany Brotcorne

Malgré leur proximité génétique, les chimpanzés (*Pan troglodytes*) et les bonobos (*Pan paniscus*) présentent des différences significatives dans leurs comportements sociaux. Il est alors légitime de se demander si leurs réponses au stress diffèrent également. Cependant, peu d'études comparent ces deux espèces, surtout à travers l'analyse d'observations comportementales. Nous avons donc utilisé des observations focales et toutes occurrences pour examiner les taux de quatre comportements de substitution — l'auto-grattage vigoureux, l'auto-grattage doux, le bâillement et l'essuyage de nez — qui sont connus pour être liés au stress. Contrairement aux attentes, les chimpanzés n'ont pas produit davantage de comportements liés au stress que les bonobos (à l'exception du bâillement), et les différences entre les groupes étaient plus marquées. Les faibles corrélations entre les quatre comportements (à l'exception des auto-grattages vigoureux et doux chez les chimpanzés) suggèrent que le stress peut être perçu de manière variée et refléter différents niveaux d'excitation. Des facteurs tels que le sexe, l'âge et l'agression reçue influencent les comportements de substitution dans les deux espèces. Notamment, les femelles chimpanzés présentent des niveaux plus élevés d'auto-grattage vigoureux et doux que les mâles, tandis que chez les bonobos, les mâles montrent des niveaux plus élevés d'autoscratching doux par rapport aux femelles, ce qui reflète les différences dans la structure sociale des deux espèces. Les individus plus âgés affichent des niveaux de comportements de substitution plus faibles que les jeunes, suggérant une meilleure régulation du stress avec l'âge. L'agression reçue est liée uniquement à l'auto-grattage doux, soulignant l'importance du contexte dans lequel ces comportements se manifestent. Cette recherche met en évidence la nécessité d'une approche holistique pour étudier les comportements liés au stress.

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TABLE OF CONTENTS:

1. INTRODUCTION

1.1 Generalities

Humans are often considered unique due to their advanced social structures, cooperative behaviors, and complex communication systems distinguishing them from other primates (Tomasello et al., 2005; Tomasello & Herrmann, 2010). However, the evolutionary processes that led to these distinctive traits remain unclear. The fossil record provides limited evidence about behavioral ancestral states, making it challenging to trace their development over time. To try and overcome this limitation, researchers rely on studying closely related primate relatives, whose behaviors offer valuable insights into the evolutionary roots of human sociality and cooperation. These observations provide a comparative basis to infer the evolutionary developments that may have occurred in our lineage, offering a window into the social and cooperative behaviors that eventually emerged in humans.

The *Hominidae* family (also known as great apes) contain eight species including *Homo sapiens* and among them, two are particularly interesting to study for gaining insights into human nature: bonobos (*Pan paniscus*) and chimpanzees (*Pan troglodytes*) (Prado-Martinez, 2013). They are sister species belonging to the genus *Pan* and their common ancestor is the closest living relative to our *Homo sapiens* species (Prado-Martinez, 2013). Due to their close genetic relatedness, these species share similarities in morphology, feeding adaptations and social systems (Hare & Wrangham, 2017). However, they are also fairly different in multiple aspects, especially regarding their social behavior. Let us examine these similarities and differences, and explore the evolutionary mechanisms that may have contributed to their development.

1.1.1 *Geographic distribution and phylogeny*

Chimpanzees and bonobos diverged from each other roughly one to two million years ago (Prado-Martinez, 2013, Fig.2). The Congo River is suggested to be responsible for the evolutionary split, as great apes are less adept swimmers compared to other mammals of similar size (Eriksson et al., 2004). This spatial divergence led to an ecological divergence in the two species, which potentially lies at the basis of their rather distinct socio-behavioral patterns.

Chimpanzees dispersed north of the Congo River (Fig.1), and inhabit a wide range from East to West Africa (J. A. M. Thompson, 2003), with four known subspecies: the Western chimpanzee (*Pan troglodytes verus*); the Nigeria-Cameroon chimpanzee (*P. t. ellioti*); the Central chimpanzee (*P. t. troglodytes*); and the Eastern chimpanzee (*P. t. schweinfurthii*). Bonobos on the other hand, are not divided into subspecies and endemic to the Democratic Republic of the Congo only (Eriksson et al., 2004, Fig.1).

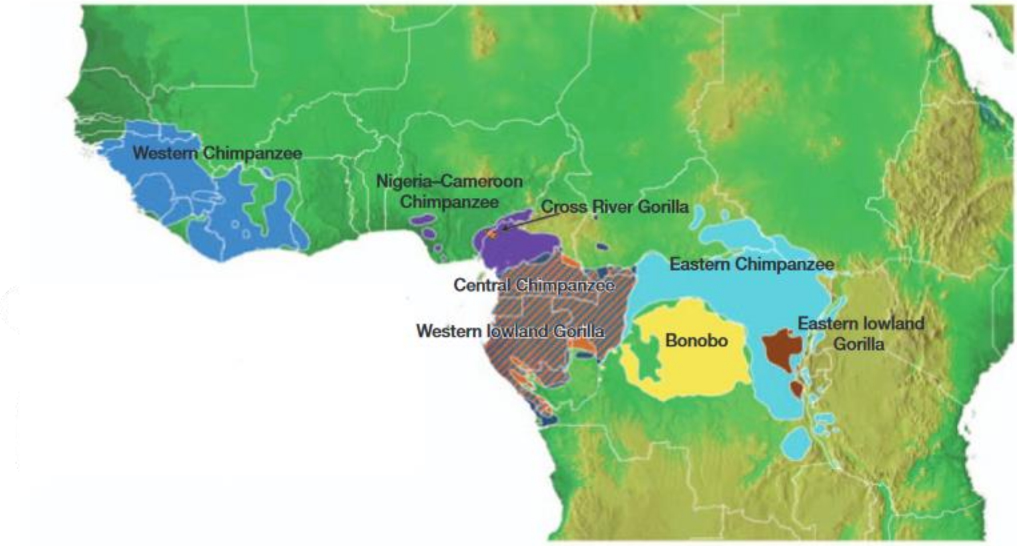


Fig.1: Geographical distribution of great ape populations across Central Africa (Padro-Martinez, 2013).

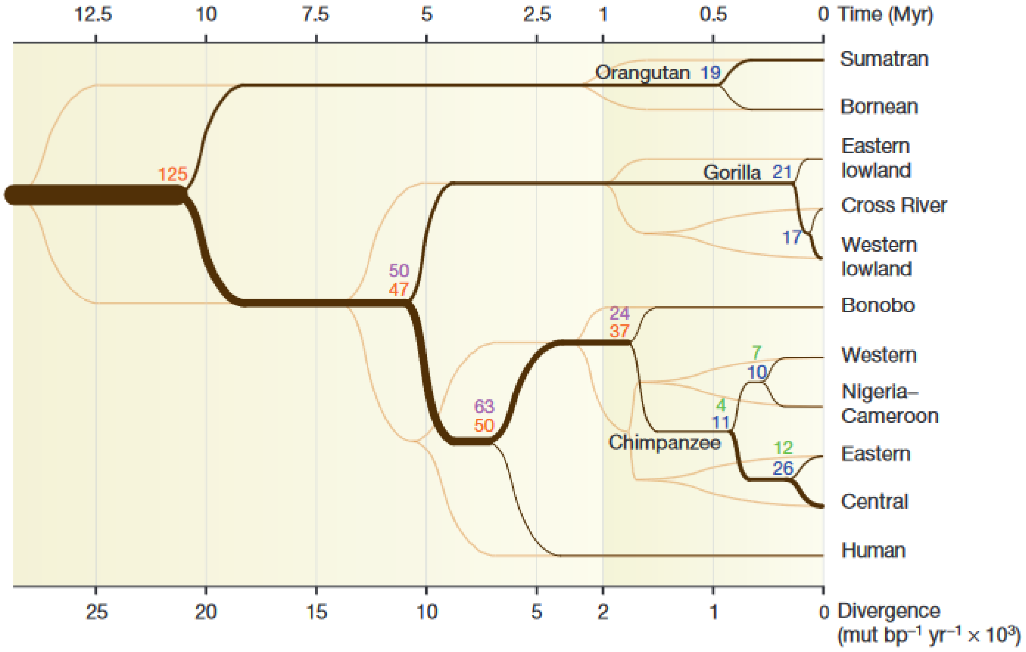


Fig.2: Population splits during great ape evolution (Padro-Martinez, 2013).

1.1.2 Similarities between the two species

Bonobos and chimpanzees both live in multimale and multifemale groups characterized by fission-fusion dynamics that tend to rely on ecological factors like food availability (Boesch et al., 2002). Chimpanzees and bonobos exhibit dietary similarities, both being omnivorous with a pronounced preference for fruits and plant-based foods (Kano & Mulavwa, 1984; Tutin & Fernandez, 1993). Fruits provide them with essential vitamins and energy and in addition, they consume various plant tissues such as leaves, stems, and bark, which offer necessary fibres and nutrients. This plant-based diet is complemented by the intake of invertebrates, adding protein and other essential nutrients (Caroline et al., 1992). Furthermore, both species occasionally hunt and consume mammalian prey (Tutin & Fernandez, 1993), incorporating a carnivorous aspect into their otherwise primarily herbivorous diet. This reflects their ecological versatility and ability to exploit a wide range of food resources within their habitats.

Females tend to emigrate in both species to avoid inbreeding (especially with their fathers) while males are philopatric (Goodall, 1986 ; Kano, 1992 ; Pusey, 1980) and in both species males maintain linear dominance hierarchies, with high-ranking individuals mating at higher frequencies (Surbeck et al., 2011). Both species are also classified as endangered on the IUCN Red List since 1996 (https://www.iucnredlist.org/).

1.1.3 Behavioral differences between the two species

Despite their close evolutionary relationship and morphological and socio-ecological similarities, chimpanzees and bonobos also exhibit notable behavioral differences. The main difference being that chimpanzees live in male-dominated societies while bonobos live in female-dominated ones (Boesch, 2009; Surbeck et al., 2011). Male chimpanzees form strong social bonds that aid in the maintenance of the dominance hierarchy, and show aggressive, coercive behavioral patterns towards females and agonistic, territorial interactions with neighboring communities. Bonobos, on the other hand, inhabit more food-rich environments, allowing for females to form close bonds with other females rather than compete with them over resources to raise offspring (White & Chapman, 1994). As a result, bonobo females form coalitions and exhibit intolerance towards male suppression (Hohmann & Fruth, 2003). Bonobo males do not exert sexual coercion over females, infanticide rates are low, and the majority of intergroup encounters occur without severe violence (Hare, 2012; Muller & Wrangham, 2009). Competition regarding sexual partners is also lower than in chimpanzees, as bonobos form highly gregarious socio-spatial associations, with females comprising a larger proportion of the population compared to chimpanzees (Hare, 2012). High levels of gregariousness in bonobos are thought to be at the basis of the development of higher prosociality and cooperation in this species, including more readily observed co-feeding compared to chimpanzees (Furuichi, 2011; Hare & Wrangham, 2017).

Bonobos also demonstrate more flexible social skills in cooperation and communication (Boesch et al., 2002; Hare, 2012; Hare & Wrangham, 2017; Kano & Mulavwa, 1984; Tan et al., 2017), and adult bonobos engage in more frequent play and display more playful facial expressions than chimpanzees (Palagi, 2006). Finally, they are also said to exhibit greater empathy towards conspecifics by offering more consolation (Clay & de Waal, 2013).

1.2 The self-domestication hypothesis

The main hypothesis regarding the social behaviors differences between bonobo and chimpanzee is that, due to their ecological differences, selective pressures against aggression were present in the bonobo evolutionary past.

This process was labelled "self-domestication" (Hare, 2012), as it shows similarities to the domestication process in which humans select for tameness in pets and livestock, with the sole difference that no humans were involved in the selective process that occurred in bonobos. To understand the genetic and behavioral changes that occur during this process, Dmitri Belyaev conducted studies on foxes in the mid-20th century and he showed that in just a few generations, selection against aggression did not only lower aggressive tendencies, but caused a whole set of changes in behavior, physiology, cognition and morphology, a process known as the domestication syndrome (Belyaev, 1979; Hare, 2012; Trut et al., 2009). As levels of aggression lower, morphological changes occur such as floppy ears, curly tails, reduction in the size of the crania, faces and teeth (Hare & Wrangham, 2017), as well as physiological changes such as higher serotonin levels in tamer females (Belyaev, 1979), a neurotransmitter known to inhibit aggression (Lesch & Merschdorf, 2000).

But aside from a reduction in aggressiveness, domesticated animals also tend to see an increase in prosocial behaviors (like play, non-reproductive sexual behaviors and grooming) (Hare & Wrangham, 2017; Trut et al., 2009.), and a reduction in levels of anxiety (Trut et al., 2009).

Due to their reduced aggressive tendencies compared to chimpanzees, bonobos are thus hypothesized to have undergone a similar process to domestication. Evidence to support this hypothesis, aside from differences in aggression, include that bonobos exhibit juvenilized morphology as adults, bonobos exhibit juvenilized morphology as adults, an increase in prosocial behaviors (non-reproductive sexual behaviors in both heterosexual and homosexual relationship (de Waal, 1989; Hare & Wrangham, 2017; Kano, 1992; Kuroda, 1984), grooming and play (Hare, 2012), higher serotonin levels (Staes, 2019)).

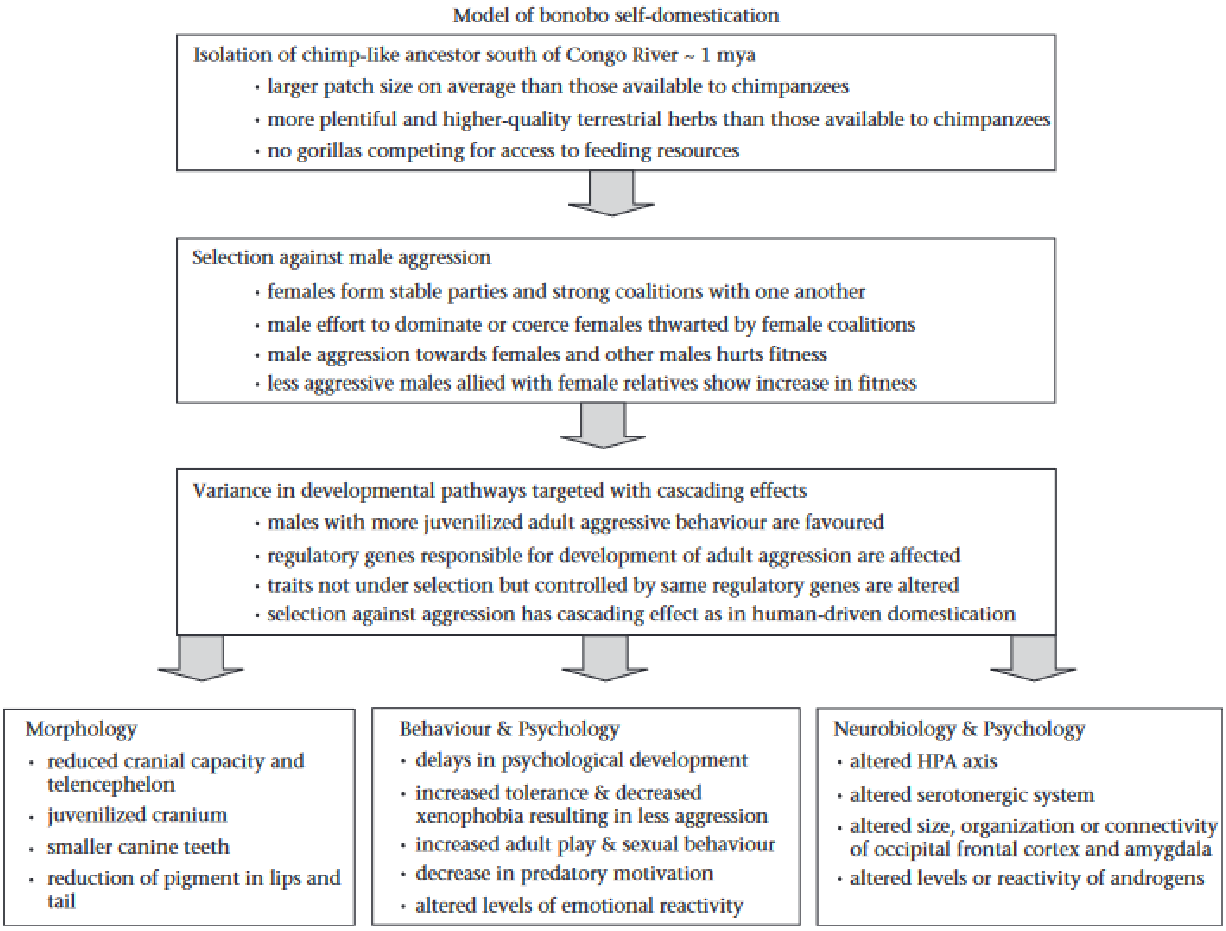


Fig.3: A model of bonobo evolution due to selection for tolerance and against aggression (Hare, 2012).

This decrease in aggression should be accompanied by a decrease of fearful behaviors, but differences in anxiety are significantly understudied in both chimpanzees and bonobos. According to the self-domestication hypothesis, bonobos would be expected to show reduced levels of anxiety compared to chimpanzees, but some studies suggest the opposite, saying that bonobos may exhibit higher levels of nervousness compared to chimpanzees (Wobber et al., 2010). For instance, during competitive situations, bonobos experience an increase in cortisol levels associated with stress, whereas chimpanzees display elevated testosterone levels linked to aggressivity (Wobber et al., 2010).

However, most studies primarily measure hormone levels and do not consider the behavioral aspect of stress. Anxiety cannot be fully understood solely through hormonal analysis, as hormones serve multiple functions. A systematic comparison of stress-related behaviors is currently lacking.

1.3 Stress

1.3.1 Stress in primates

The phenomenology of the stress syndrome involves three distinct response modalities: physiological reactions, subjective feelings and behavioral changes (Chrousos & Gold, 1992). However, the challenge in assessing stress in animals lies in the inability to directly access their subjective experiences. Consequently, researchers mostly rely on physiological indicators like cortisol, or behavioral indicators like displacement activities.

A displacement activity is defined as a behavioral pattern that happens in situations in which it is not expected to be observed (Tinbergen, 1952). They are common during fighting, agonistic contest, courtship and play in most vertebrate animals and induce anxiolytic effects (Troisi, 2002). However, as there are no morphological criteria to identify displacement activities, their identification is based almost exclusively on a contextual analysis. Displacement activities in primates differ from other types of behaviors by their higher frequency in stressful situations, their function in conflict resolution, their role in social communication and the fact that they do not require ritualization to convey information (Maestripieri, 1992).

1.3.2 Displacement activities

In primates, most displacement activities involve self-directed behaviors (SDBs) which are behaviors that encompass any actions involving self-touching, such as self-scratching, self-touching, autogrooming and nose-wiping (Maestripieri, 1992; Aureli & de Waal, 1999; Kret et al., 2016; Leavens et al., 2004). Increased levels of SDBs have been linked to frustration, uncertainty, and anxiety during social conflicts in various primate species (Maestripieri, 1992). Research indicates that anxiogenic drugs elicit increased rates of SDBs, whereas the administration of anxiolytic drugs reduces SDB rates, further supporting the relationship between SDBs and anxiety (Maestripieri, 1992; Schino et al., 1991, 1996). Notably, human patients with anxiety report engaging in elevated levels of SDBs, suggesting a cross-species similarity in the behavioral manifestations of anxiety (Fairbank & Keane, 1982; Waxer, 1977). Thus, SDBs can be viewed as both a symptom and a response to stress and anxiety across different species. But not all displacement behaviors are self-directed behaviors or behaviors that involve self-touching. In primates, yawning is also shown to increase in response to emotional stress (Maestripieri, 1992; Troisi, 2002; including chimpanzees (Baker & Aureli, 1997; Kutsukake, 2003), long-tailed macaques (Schino et al., 1988 ; Troisi, 1990), Anubis baboons (Easley et al. 1987), Japanese macaques (Troisi, 1990), hamadryas baboons (Kummer, 1968) and stumptailed macaques (Bertrand, 1969)).

Scratching and autogrooming are easily observable body care activities in primates and are among the most commonly reported displacement activities (scratching : chimpanzees (Lawick & Goodall, 1972, Aureli & de Waal, 1997; Baker & Aureli, 1997 ; Kutsukake , 2003), bonobos (Laméris, 2022), hamadryas baboons (Kummer, 1968), stumptailed macaques (Bertrand, 1969), rhesus macaques (Diezinger & Anderson 1986), anubis baboons (Easley et al., 1987), long-tailed macaques (Schino et al., 1988 ; Aureli & Schaik, 1989) ; autogrooming : chimpanzees (Aureli & de Waal, 1999; Baker & Aureli, 1997; Kutsukake, 2003; Van Lawick-Goodall, 1973), stumptailed macaque (Goosen, 1974; Lopez-Vergara et al., 1989) , Java monkeys (Clark & Smith, 2013), long-tailed macaque (Schino et al., 1988 ; Troisi, 1990 ; Aureli & van Schaik, 1991)). Scratching, specifically, has been associated with conflict, frustration and anxiety in multiple *Pan* studies (Lawick & Goodall, 1972, Aureli & de Waal, 1997; Baker & Aureli, 1997, Kutsukake, 2003).

Chimpanzees will show higher levels of self-scratching and yawning in contexts of social tension or anxiety. Indeed, rates of displacement activities increased after hearing loud vocalizations from neighboring groups of conspecifics, which are associated with increased risks of intragroup aggression (Baker & Aureli, 1997). Neighbor vocalizations serve as effective stimuli because they allow researchers to measure an individual's response to potential anxiety without any direct event occurring to the subject. By using these vocalizations, scientists can observe how the subject's behavior changes purely due to their emotional state. This method avoids the influence of actual events that might otherwise affect the subject's level of activity (Baker & Aureli, 1997). Aggression is also frequently associated with higher levels of yawning and scratching and positive correlations are seen in top-raking male chimpanzees between displaying rates and self-scratching (Boekhorst et al., 1991). Scratching rates of adult male chimpanzees also increase with higher levels of reproductive competition (this means that the fewer estrus females present in the group, the more frequently the male engages in both rough and gentle autoscratching behaviors) (Boekhorst et al., 1991) and displacement activities like yawning and rough self-scratching increased under more crowded conditions in captivity (Aureli & de Waal, 1997).

SDBs also increase in chimpanzees with increasing complexity of cognitive tasks (Leavens et al., 2004), with longer duration of complex tasks (Clark & Smith, 2013), when more errors or made (Yamanashi & Matsuzawa, 2010) or when tasks have unpredictable outcomes (Leavens et al., 2001). Moreover, in a study done on a 7-year-old female chimpanzee, rates of SDBs increased when a negative reinforcer (a buzzer) was activated but not when a secondary positive reinforcer (a chime) was (Tomonaga et al., 1993), suggesting that an anxiety-inducing situation is correlated to increased SDBs. This chimpanzee was reported to scratch, self-groom, and face-stroke when making errors during the learning phase of tasks.

In bonobos, very little reports can be found on self-directed behaviors. One study showed an increase in nose-wiping behavior potentially caused by frustration during cognitive testing (Kret et al., 2016). Another found that in contrast to expectation, bonobos tend to yawn less during periods immediately following social stress (Demuru & Palagi, 2012). In addition, some bonobo displacement behaviors might also reflect different levels of stress severity, with nose-wiping potentially reflecting relatively low arousal increases, while rough self-scratching reflects higher levels of arousal (Laméris et al., 2022). Interestingly, bonobos exhibit more nose-wiping than rough self-scratching during cognitive tasks, whereas chimpanzees display more rough self-scratching than nose-wiping, which might indicate higher arousal levels in chimpanzees compared to bonobos, supporting the self-domestication hypothesis. However, most studies mentioned above suffer from small sample sizes (N=3 in Wagner et al., 2016, N=1 in Leavens, 2004, N=8 in Laméris, 2022, N=4 in Kret, 2016) and involve studying apes while they are performing specific tasks (Laméris et al., 2022; Leavens et al., 2004; Wagner et al., 2016). More research is needed to study baseline levels of stress of individuals living their daily lives in large samples. Additionally, there are very few studies employing uniform data collection methods across both species, making it difficult to compare results in chimpanzees and bonobos directly (Staes et al., 2022; van Leeuwen et al., 2023).

These latter studies also find that chimpanzees and bonobos exhibit a remarkable degree of behavioral flexibility (Staes et al., 2022; van Leeuwen et al., 2023). This flexibility allows individuals within the same group to display a wide range of behaviors, influenced by factors such as social dynamics, environmental conditions, and individual personalities. Bonobo dyads, for example, have been shown to vary greatly in pro sociality when food is involved with many dyads showing no prosociality whatsoever, thereby contesting the popular view of the prosocial and food sharing bonobo (Verspeek et al., 2022). Some studies have found that these two species might not differ as much as it was thought and that intragroup variations might be higher than intraspecies ones, thereby stressing that large multi-group studies are needed to make species generalizations. Studies regarding co-feeding tolerance, for example, showed that intergroup variations in bonobos and chimpanzees were higher than interspecies ones (Staes et al., 2022; van Leeuwen et al., 2023). Therefore, the commonly emphasized dichotomy between the two *Pan* species requires a more nuanced understanding.

1.3.3 *Factors influencing displacement activities*

Individual differences in SDBs can be caused by a variety of factors, like the levels of aggression they receive which is often sex or rank dependent. In both species, levels of scratching (especially rough autoscratching) and yawning increase as aggression rates increase (Anestis et al., 2006), for example during times of high density (Aureli & de Waal, 1999). Female chimpanzees also appear to respond to high population density differently than males, often reducing affiliative behavior to mitigate aggression (Videan & Fritz, 2007). Consequently, it is reasonable to anticipate that their stress levels may also differ as a result. Rates of rough autoscratching even increase in female chimpanzees when they were around other group members, which is not the case in males (Kutsukake, 2003), indicating a sex bias in the expression of SDBs can be expected. However, other studies suggest the opposite, that male chimpanzees have higher rates of stress levels than females. Observational studies found that male chimpanzees have higher rates of autoscratching and autogrooming than female chimpanzees (Koski, 2011) and that scratching rates (no distinction between gentle autoscratching and rough autoscratching was made) were higher in males after conflicts than among females (Koski et al., 2007). In bonobos, no studies have been performed to our knowledge investigating sex-effects on levels of displacement behaviors. However, a study looking at hair-plucking (another displacement behavior) in bonobos found that in females, the percentage of self-directed plucking was positively correlated with urinary cortisol levels, while in males, a strong negative trend was observed (Brand et al., 2016). By proxy, a sex difference in bonobos regarding displacement behaviors might also be expected.

In some primate species rank, rather than aggression received may be linked with higher stress. The question remains whether low or high rank would cause more stress and both have been documented in baboons (Sapolsky, 1992; Sapolsky, 2005). In chimpanzees, aggression received appears to have a higher effect in glucocorticoid levels in male chimpanzees than rank (Muller et al. 2021). Surprisingly, very little literature could be found on the factors causing variation in nose-wiping behaviors in either species.

Finally, despite considerable research into stress and cortisol regulation, there remains a notable gap in understanding the effects of age on stress, particularly in relation to behavioral stress. Existing studies present conflicting findings, with Thompson (2010) reporting increased urinary cortisol levels in reproductive female chimpanzees, while Anestis (2006) observed decreased serum cortisol levels with aging in chimpanzees and studies remain to be done about age effect on stress in bonobos. Expanding research on age effect on stress is then crucial to better understand how it influences the rates of displacement behaviors.

1.4 Aims of the study

The aim of this study is to systematically compare the rates of four displacement activities (rough autoscratching, gentle autoscratching, nose wiping and yawning) in the two *Pan* species, chimpanzees and bonobos, as well as the factors influencing these rates.

The first aim of this study is then to determine the existence of significant differences in displacement behaviors at the species level and to see whether bonobos show indeed less displacement activities and therefore stress than chimpanzees do.

- **Hypothesis 1**: Following the self-domestication hypothesis where selection against aggression causes overall lower reactive behaviors in bonobos including aggression and stress, bonobos are expected to show lower levels of displacement behaviors than chimpanzees, meaning that it is expected that they score lower levels on all of them. It is especially the case for behaviors representing severe arousal (like rough autoscratching) than not severe arousal. Moreover, yawning is expected to indicate negative arousal in chimpanzees but positive arousal in bonobos.

The second aim of this study is to compare different groups within each species to help ascertain whether group differences outweigh species differences.

- **Hypothesis 2**: Group differences in displacement behaviors outweigh species differences, indicating both species have large behavioral flexibility. This is expected for all four behaviors.

The third aim of this study is to identify underlying factors that influence variations in displacement behaviors at an individual level (sex, age and aggression received).

- **Hypothesis 3**: Low-ranking individuals (with these being females in chimpanzees and males in bonobos) experience more stress and thus sex is the main explanatory factor in displacement behavior variation with female chimpanzee and male bonobos showing higher levels.
- **Hypothesis 4**: Since Thompson (2010) exclusively studied cortisol levels in reproductive female chimpanzees, we align our expectations with the findings of Anestis (2006), who demonstrated that stress levels, as indicated by serum cortisol,

tend to decrease with age in chimpanzees. therefore, age is expected to decrease the rates of displacement behaviors in chimpanzees and bonobos.

- **Hypothesis 5**: The aggression an individual receives is positively correlated with the rates of displacement behaviors it displays as aggression is known to increase under stress-inducing conditions.

2. MATERIAL AND METHODS

2.1 Study subjects and housing

Behavioral data were collected for 71 bonobos (46 females and 25 males, Annex 1) divided in 8 groups in 6 different zoos in Europe (Apenheul, Frankfurt, Ouwehands, Planckendael, Stuttgart and Vallée des Singes) from the years 2021 to 2022. Chimpanzees data was collected in 2023 and 2024 for 37 individuals (24 females and 13 males, Annex 2) in a total of 4 European zoos (Dierenrijk, Antwerp, Beauval, and Bussolengo). For both species all individuals were adults or subadult (age 7 years old and up). All individuals were housed in multi-male/multi-female groups with some groups being managed in a fission-fusion system during the day (Apenheul, Beauval and Planckendael). Individuals had access to inside and/or outside enclosures depending on the weather conditions.

2.2 Data collection

Behavioral data was recorded mostly live using a laptop with software The Observer XT (Noldus, The Netherlands, version 14) during observations or through coding of video or audio recording afterwards. Observations were performed by 12 students, with each student receiving two to five weeks of training until animal recognition went smoothly and the species-specific ethogram (Stevens, J., Staes, N., & Verspeek, J. (2023)) and coding protocol were mastered. The ethogram is based on several existing ethograms, mostly on Jordan (1977); de Waal (1988); Vervaecke et al. (1999, 2000) and the unpublished ethogram at Planckendael.

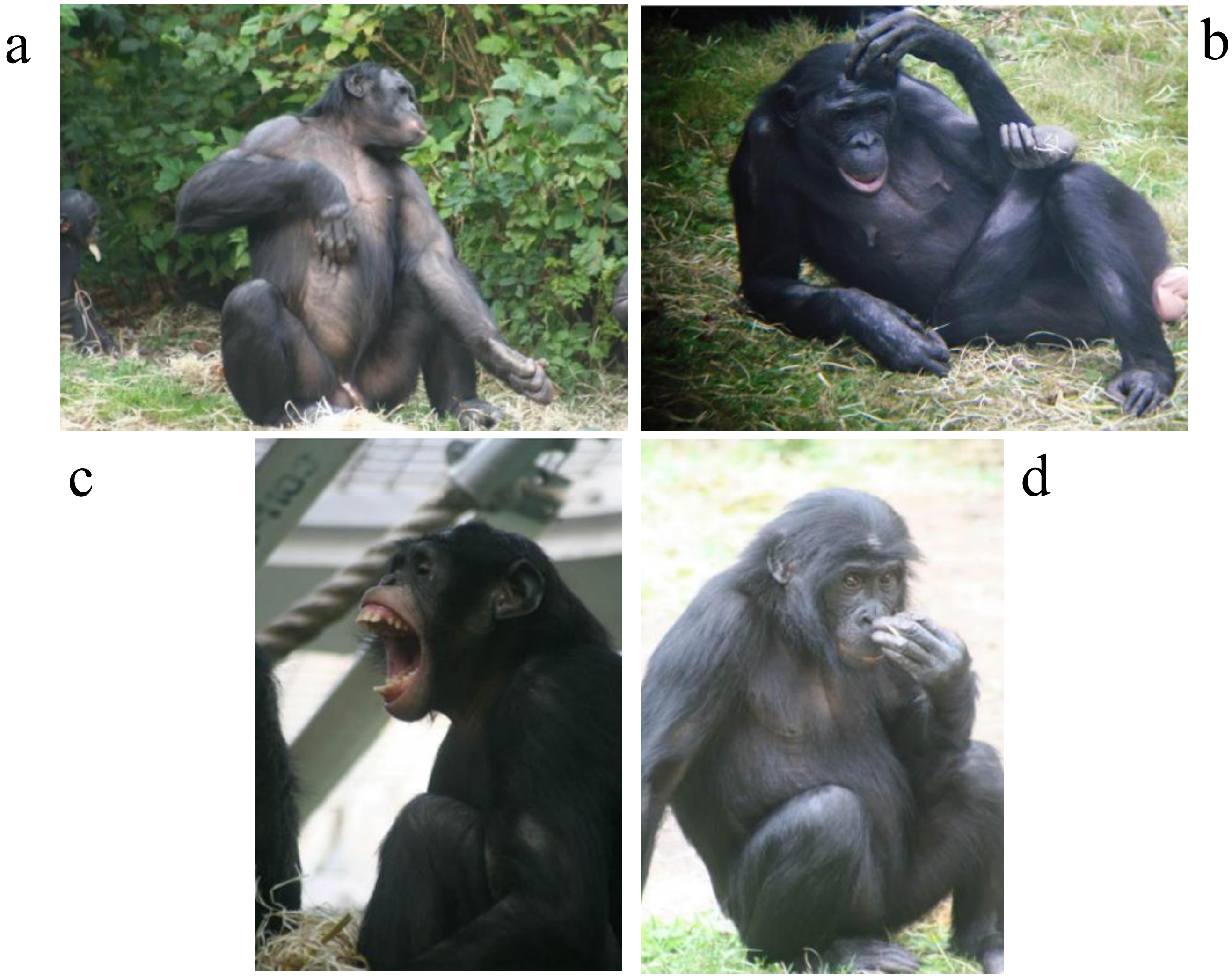
Since behavioral data was recorded by different people, inter-observer reliability was tested at the end of the training weeks by coding the same 10-minute video of bonobo behavior. A mean of r = 0.85 was achieved by all observers, indicating high interobserver reliability (Martin & Bateson, 2007) .

Four behaviors were observed for this study to determine stress in chimpanzees and bonobos, using 10-minute focal observations: rough and gentle self-scratching, nose wiping and yawning (for definitions see Table 1 and for visual representation, see Fig.4). Focal data consist of recording all the behaviors that one individual performs for a duration of 10 minutes, and the behaviors that others do to the focal individual (Altmann, 1974). If an individual was out of sight for over 3 minutes, the sampling had to be interrupted and picked up again once the individual returns to sight. To investigate the association between stress and levels of aggression received, agonistic interactions were also recorded ad libitum during focal observations (even if the focal individual was not involved), and during feeding times when focal observations were paused and the scoring method was switched to group observations to focus solely on agonistic interactions due to these interactions then occurring more frequently.

Table 1: Definitions of the displacement behaviors used to determine stress in chimpanzees and bonobos (“S” stands for “subject”).

Behavior	Definition	Point event / duration
Rough self-scratching	S rakes one’s own hair or skin with fingernails including mainly movements of hand or fingers	Duration and point event
Gentle self-scratching	S rakes one’s own hair or skin with fingernails including large movements of the arm	Duration and point event
Nose wiping	S raises the arm, while the hand is relaxed, and moves the wrist downwards on the nose / S wipes his nose, by using his wrist.	Point event
Yawning	Open mouth and exposed teeth in a gaping movement	Point event

Fig.4: Visual representation of the displacement activities used to determine stress in chimpanzees and bonobos



a) Rough autoscratching, b) gentle autoscratching, c) yawning, d) nose wiping. (Stevens, J., Staes, N., & Verspeek, J. (2023)).

For bonobos, an average of 12.1 hours per focal individual were taken (range 8.3 to 14.6 hours) and an average of 13 hours of all occurrence per group (from 4.1 to 17.6 hours) were taken. For chimpanzees, an average of 15.5 hours of focal (from 3.5 to 22.6 hours) was recorded per individual and 36.37 hours of all occurrences (from 14.26 to 45.08 hours) per group for chimpanzees. All five behavioral variables were considered as point events (not durations) and in the statistical analysis they were corrected for time observed. For stress behaviors this means that total focal time was taken into account, while for aggression received, all focal times were added to the time of all occurrence observations during feeding.

2.3 Data analysis

Different models were constructed in R Studio (version 4.1.1) to investigate how each stress behavior (Table 1) differed between species, groups, by sex or depend on aggression received or sex ratio of the social group.

General mixed linear models were used (package glmmTMB in RStudio (Brooks, 2017)) to identify factors that explain variation in the four behavioral variables associated with stress (rough autoscratching, gentle autoscratching, yawning and nose wiping, (Table 2)). To account for differences in time observed per individual, all models were corrected for individual time observed using the function (offset=log(FocalTime)). A drop test was then used to detect non-significant explanatory variables and delete them from the model. A dispersion test and a zero-inflation test were then used on the model to test for the relevance of the model. If the glm model was overdispersed and/or zeroinflated, a negative binomial test was used. AICs were used to compare models created with null model (=model with only the random effect) to assess for the goodness of fit of the model, with a lower AIC indicating a better model fit.

First, we analyzed if the rates of the different stress behaviors differed between species (variable with 2 levels: chimpanzee and bonobo). One model per behavior was constructed and group (variable with 12 levels: the 12 different zoo groups) was added as a random effect to correct for the fact that individuals living in the same zoo were not independent of the other individuals that have been observed in that same zoo. Plots of the displacement behaviors were corrected for the time observed (calculated as the amount of each displacement behavior per observed). Pearson correlations within species for the four displacement behaviors has been calculated through the cor.test function.

Secondly, we analyzed if the rates of the different stress behaviors differed between groups (variable with 12 levels). The emmeans function (library emmeans) was used to investigate the results of the comparisons between the different groups (Lenth et al., 2023). Fitted values were then used to represent the predicted values and boxplots were created from them to visualize the model.

Thirdly, we examined whether the effects of sex (variable with two levels: female and male) could be species-dependent by analyzing the interaction between the species variable (variable with two levels) and the sex variable and the effect of aggression received and age (numeric variables, see table 2). Group was also included as a random effect. The emmeans function was used to explore and compare the effects of different levels of the interaction between species and sex, adjusting for the fact that multiple comparisons are being made. Fitted values were then used to represent the predicted values and boxplots using the function ggplot2 were created from them to visualize the model.

Table 2: Factors that were tested

Variables	Value
Species	Chimpanzee or Bonobo
Group	Apenheul, Frankfurt, Ouwehand, Planckendael, Stuttgart, Vallée des Singes, Dierenrijk, Antwerp, Beauval, and Bussolengo
Sex	Male or Female
Age	Elapsed time between the birth of the individual and the beginning of the observations.
Aggression Received	Quantity of agonistic interactions received: pest aggression, aggressive intention, short charge, long charge, direct display, mutual display, parallel display (for the definition of all agonistic interactions, see table 3)

Table 3: Ethogram for aggressive behaviors, S means "subject" and R means "receiver".

Behaviour	Definition
Pest aggression	A behavior sequence starting as pestering (S repeatedly approaches R, throws objects, swings over R, etc. without the intention to withdraw and without play face) in which pilo-erection occurred
Aggressive intention	Sudden tense hand or body movements in the direction of another individual in non-playful contexts or hitting, kicking, etc… without locomotion
Short charge	S shows tensed running at R over a few meters (up to five steps)
Long charge	S shows tensed running at R over more than a few meters (more than five steps)

Direct display	Tensed running in the direction of, parallel to or closely passing by another individual, usually while pushing an object. This can end in a collision or other contact aggression.
Mutual display	Two individuals perform a direct display towards each other
Parallel display	S and R perform a display alongside each other, running in the same direction

3. RESULTS

3.1 Do bonobos and chimpanzees differ significantly in their displacement activities?

Three out of four displacement activities did not differ between species (rough self-scratching (F(1,6) = 1, p = 0.8089), gentle self-scratching (F(1,6) = 1, p = 0.2386) and nose wiping (F(1,6) = 1, p = 0.8678), except for yawning (F(1,6) = 1, p = 0.01826) (Annex 3). Chimpanzees did more yawning (est = 0.5153, p = 0.0058) than bonobos did.

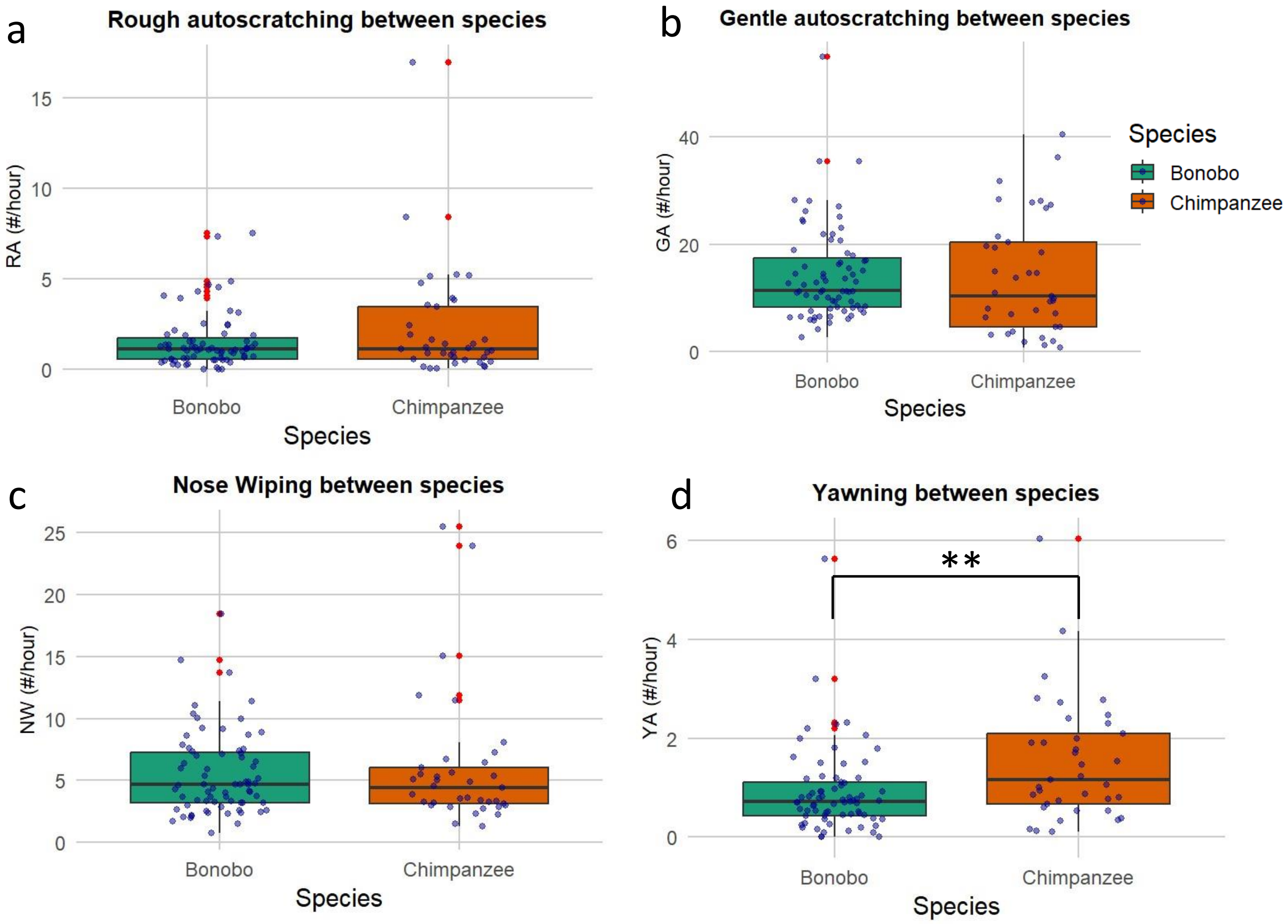


Fig. 5. Comparison of the different displacement activities between the two species. The x-axis represents the two species: bonobos (green) and chimpanzees (orange) while the y-axis represents the displacement activity corrected for the time observed per individual. A) rough autoscratching, b) gentle autoscratching, c) nose wiping, d) yawning

Rough autoscratching and gentle autoscratching highly correlated with each other (r = 0.76, p = 3.54e-08, Table 4) in chimpanzees while they did not in bonobos (r = 0.08, p = 0.52, Table 5).

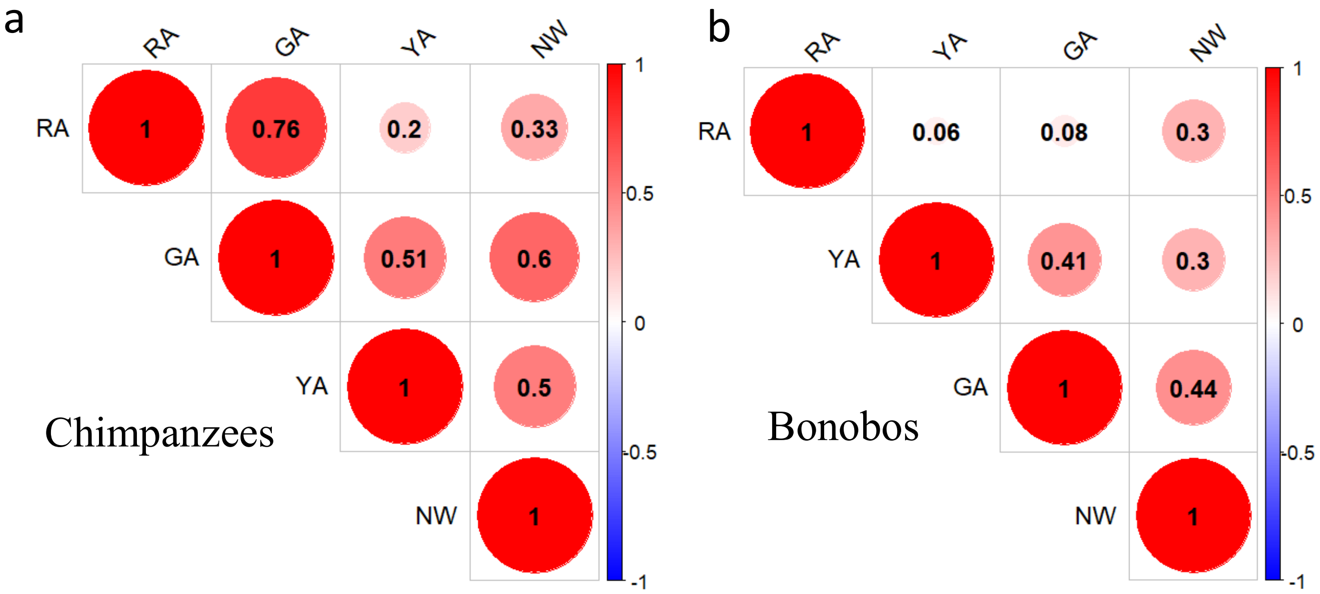


Fig. 6: Correlations within species for the four displacement behaviors. Abbreviations: rough autoscratching (RA), gentle autoscratching (GA), nose wiping (NW), yawning (YA). a) correlations in chimpanzees, b) correlations in bonobos

Table 4: Matrix of correlations between displacement behaviors in chimpanzees and the p-value associated. p ≤ 0,001: ***, p ≤ 0,01: **, p ≤ 0,05: *, p > 0,05: no *.

	RA	**GA**	**YA**	**NW**
RA	1			
GA	0.76***	1		
YA	0.2	0.51***	1	
NW	0.33*	0.6***	0.5***	1

Table 5: Matrix of correlations between displacement behaviors in bonobos and the p-value associated. p ≤ 0,001: ***, p ≤ 0,01: **, p ≤ 0,05: *, p > 0,05: no *.

	RA	**GA**	**YA**	**NW**
RA	1			
GA	0.08	1		
YA	0.06	0.41***	1	
NW	0.3**	0.3***	0.44**	1

3.2 Do group differences outweigh species differences?

Rates of the four displacement behaviors differed significantly between groups (Rough autoscratching: F(1,6) = 11, p = 1.58e-11, gentle autoscratching: F(1,6) = 11, p < 2.2e-16, yawning: F(1,6) = 11, p = 0.004353, nose wiping: F(1,6) = 11, p = 8.916e-08, Fig.7) (Annex 4). However, post-hoc comparisons between dyads between groups show that only one dyad differed significantly in their yawning rates (Table 8) while multiple dyads differed significantly in the rates of rough autoscratching (Table 6), gentle autoscratching (Table 7) and nose wiping (Table 9).

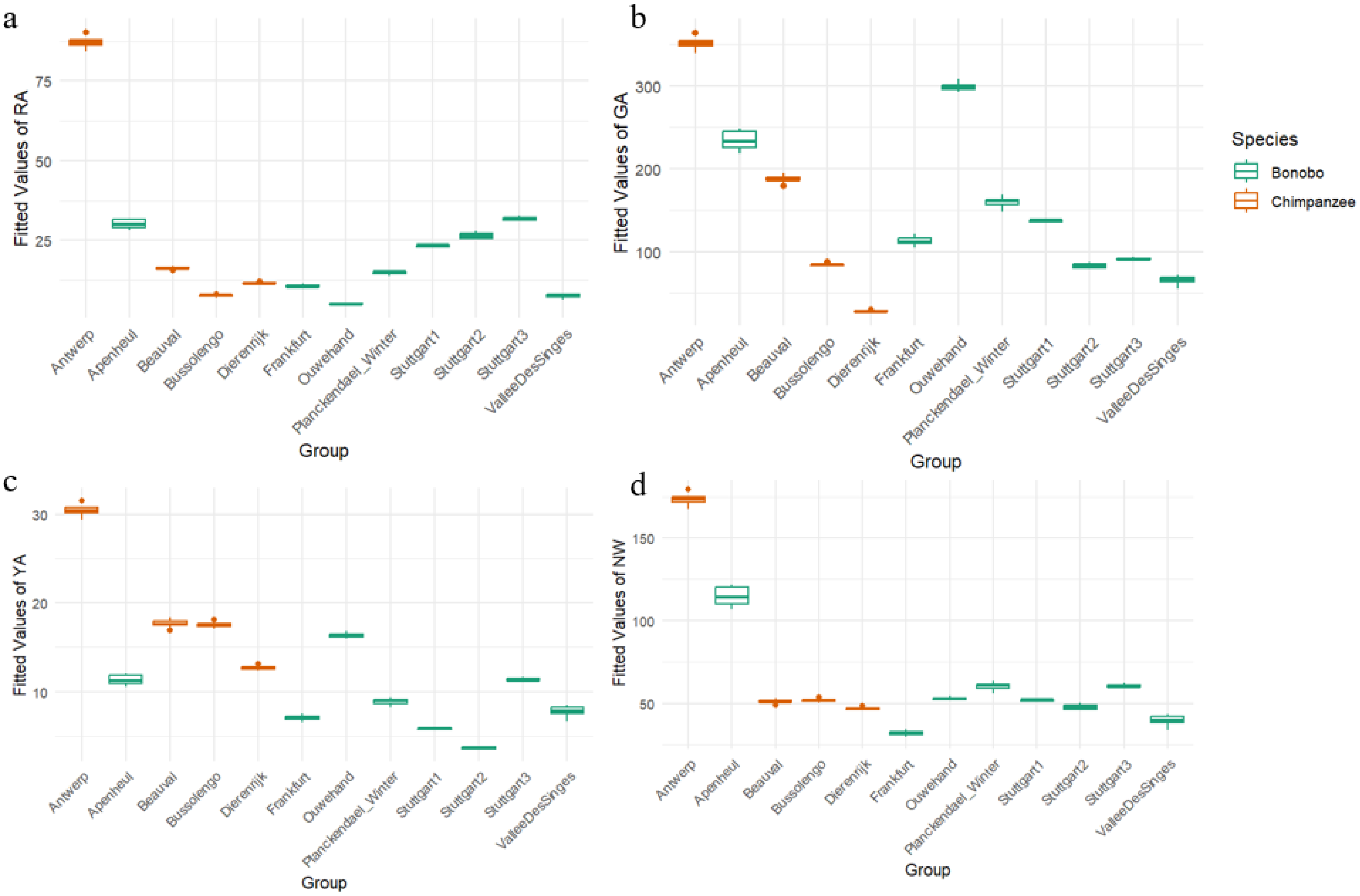


Fig. 7: Comparison of the fitted values of the four displacement behavior in the twelve different groups. Abbreviations: rough autoscratching (RA), gentle autoscratching (GA), nose wiping (NW), yawning (YA). The x-axis represents the different groups (zoos) of the two species while the y-axis represents the fitted values of the displacement behavior. A) Rough autoscratching, B) gentle autoscratching, C) yawning, D) nose wiping.

Table 6: Post-hoc comparisons between groups regarding the rates of rough autoscratching. Only the significant dyads (p-value ≤ 0.05) were kept. Refer to annex 6 for a complete overview of all post-hoc comparisons between groups.

Dyads	**Estimate**	**SE**	**z.ratio**	**p-value**
Antwerp$_c$ - Beauval$_c$	1.0284	0.288	3.565	0.0188
Antwerp$_c$ - Bussolengo$_c$	2.33	0.357	6.525	<.0001
Antwerp$_c$ - Dierenrijk$_c$	1.625	0.367	4.431	0.0006
Antwerp$_c$ – Frankfurt$_b$	1.6547	0.299	5.533	<.0001
Antwerp$_c$ – Ouwehand$_b$	2.3609	0.33	7.144	<.0001
Antwerp$_c$ - Planckendael_Winter$_b$	1.2751	0.295	4.32	0.0009
Antwerp$_c$ – ValleeDesSinges$_b$	1.6435	0.288	5.713	<.0001
Apenheul$_b$ - Bussolengo$_c$	1.7855	0.373	4.783	0.0001
Apenheul$_b$ – Frankfurt$_b$	1.1103	0.318	3.488	0.0245
Apenheul$_b$ – ValleeDesSinges$_b$	1.099	0.308	3.573	0.0183
Beauval$_c$ - Bussolengo$_c$	1.3016	0.353	3.686	0.0122
Beauval$_c$ – Ouwehand$_b$	1.3325	0.326	4.086	0.0026
Bussolengo$_c$ – Stuttgart1$_b$	-1.5253	0.431	-3.542	0.0204
Bussolengo$_c$ - Stuttgart2$_b$	-1.9912	0.43	-4.636	0.0002
Bussolengo$_c$ - Stuttgart3$_b$	-1.9543	0.499	-3.918	0.0051
Frankfurt$_b$ - Stuttgart2$_b$	-1.316	0.383	-3.439	0.0289
Ouwehand$_b$ - Planckendael_Winter$_b$	-1.0858	0.332	-3.27	0.0498
Ouwehand$_b$ - Stuttgart1$_b$	-1.5562	0.409	-3.806	0.0078
Ouwehand$_b$- Stuttgart2$_b$	-2.0221	0.408	-4.961	<.0001

Ouwehand$_b$- Stuttgart3$_b$	-1.9853	0.48	-4.135	0.0021
Stuttgart2$_b$ - ValleeDesSinges$_b$	1.3048	0.374	3.491	0.0243

$_b$: group consisting of bonobos. $_c$: group consisting of chimpanzees

Table 7: Post-hoc comparisons between groups regarding the rates of gentle autoscratching. Only the significant dyads (p-value ≤ 0.05) were kept. Refer to annex 7 for a complete overview of all post-hoc comparisons between groups.

Dyads	**Estimate**	**SE**	**z.ratio**	**p-value**
Antwerp$_c$ - Bussolengo$_c$	1.3279	0.188	7.082	<.0001
Antwerp$_c$ - Dierenrijk$_c$	2.1279	0.207	10.285	<.0001
Antwerp$_c$ - Frankfurt$_b$	0.6807	0.16	4.242	0.0013
Antwerp$_c$ - ValleeDesSinges$_b$	0.8704	0.154	5.658	<.0001
Apenheul$_b$ - Bussolengo$_c$	1.4387	0.196	7.356	<.0001
Apenheul$_b$ - Dierenrijk$_c$	2.2386	0.214	10.451	<.0001
Apenheul$_b$ - Frankfurt$_b$	0.7914	0.17	4.66	0.0002
Apenheul$_b$ - ValleeDesSinges$_b$	0.9811	0.164	5.998	<.0001
Beauval$_c$ - Bussolengo$_b$	1.3486	0.183	7.387	<.0001
Beauval$_c$ – Dierenrijk$_c$	2.1486	0.202	10.615	<.0001
Beauval$_c$ - Frankfurt$_b$	0.7013	0.155	4.535	0.0004
Beauval$_c$ - ValleeDesSinges$_b$	0.891	0.148	6.03	<.0001
Bussolengo$_c$ - Dierenrijk$_b$	0.8	0.227	3.521	0.0219
Bussolengo$_c$ – Ouwehand$_b$	-1.6638	0.191	-8.705	<.0001
Bussolengo$_c$ - Planckendael_Winter$_b$	-1.0334	0.185	-5.575	<.0001

Bussolengo$_c$ - Stuttgart1$_b$	-0.9068	0.228	-3.982	0.0039
Dierenrijk$_c$ - Frankfurt$_b$	-1.4472	0.205	-7.044	<.0001
Dierenrijk$_c$ - Ouwehand$_b$	-2.4637	0.21	-11.723	<.0001
Dierenrijk$_c$ - Planckendael_Winter$_b$	-1.8333	0.205	-8.947	<.0001
Dierenrijk$_c$ - Stuttgart1$_b$	-1.7068	0.244	-6.997	<.0001
Dierenrijk$_c$ - Stuttgart2$_b$	-1.5315	0.246	-6.227	<.0001
Dierenrijk$_c$ - Stuttgart3$_b$	-1.4086	0.284	-4.961	<.0001
Dierenrijk$_c$ - ValleeDesSinges$_b$	-1.2575	0.2	-6.278	<.0001
Frankfurt$_b$ - Ouwehand$_b$	-1.0165	0.165	-6.172	<.0001
Ouwehand$_b$ - Planckendael_Winter$_b$	0.6304	0.164	3.843	0.0068
Ouwehand$_b$ - Stuttgart1$_b$	0.757	0.211	3.592	0.0171
Ouwehand$_b$ - Stuttgart2$_b$	0.9323	0.213	4.375	0.0007
Ouwehand$_b$ - Stuttgart3$_b$	1.0551	0.256	4.121	0.0022
Ouwehand$_b$ - ValleeDesSinges$_b$	1.2062	0.158	7.623	<.0001
Planckendael_Winter$_b$ - ValleeDesSinges$_b$	0.5758	0.151	3.808	0.0078

$_b$: group consisting of bonobos. $_c$: group consisting of chimpanzees

Table 8: Post-hoc comparisons between groups regarding the rates of yawning. Only the significant dyads (p-value ≤ 0.05) were kept. Refer to annex 8 for a complete overview of all post-hoc comparisons between groups.

Dyads	**Estimate**	**SE**	**z.ratio**	**p-value**
Beauval$_c$ – Frankfurt$_b$	1.1179	0.302	3.700	0.0116

$_b$: group consisting of bonobos. $_c$: group consisting of chimpanzees

Table 9: Post-hoc comparisons between groups regarding the rates of nose wiping. Only the significant dyads (p-value ≤ 0.05) were kept. Refer to annex 9 for a complete overview of all post-hoc comparisons between groups.

Contrast	**Estimate**	**SE**	**z.ratio**	**p-value**
Antwerp$_c$ - Bussolengo$_c$	1.1058	0.234	4.723	0.0001
Antwerp$_c$ – Dierenrijk$_c$	0.90727	0.247	3.678	0.0126
Antwerp$_c$ - Frankfurt$_b$	1.23569	0.204	6.064	<.0001
Antwerp$_c$ - Ouwehand$_b$	0.69181	0.211	3.28	0.0482
Antwerp$_c$ - ValleeDesSinges$_b$	0.65838	0.192	3.425	0.0302
Apenheul$_b$ - Bussolengo$_c$	1.21015	0.244	4.952	<.0001
Apenheul$_b$ - Dierenrijk$_c$	1.01163	0.256	3.945	0.0046
Apenheul$_b$ - Frankfurt$_b$	1.34004	0.215	6.219	<.0001
Apenheul$_b$ - Ouwehand$_b$	0.79616	0.222	3.582	0.0177
Apenheul$_b$ - ValleeDesSinges$_b$	0.76273	0.205	3.728	0.0105
Beauval$_c$ - Frankfurt$_b$	0.66708	0.199	3.36	0.0374
Frankfurt$_b$ - Planckendael_Winter$_b$	-0.67351	0.202	-3.337	0.0402

$_b$: group consisting of bonobos. $_c$: group consisting of chimpanzees

3.3 What factors explain displacement activities variation in *Pan*?

3.3.1 Effect of the interaction of sex and species

The full model (AIC = 1780.403) was a better fit than the null model (AIC = 1861.878), indicating that rates of rough autoscratching (RA) differed significantly between sexes in a species-specific matter (F(1,6) = 1, p = 7.218e-15, Table 10). Specifically, male bonobos engaged in higher rates of RA compared to female bonobos (est = 0.4546, SE = 0.0619, p <.0001, Table 11), whereas female chimpanzees exhibited higher RA rates than male chimpanzees (est = 0.2070, SE = 0.0580, p = 0.0020, Table 11).

The full model (AIC = 3454.167) was a better fit than the null model (AIC = 3613.344), indicating that rates of gentle autoscratching (GA) differed significantly between sexes in a species-specific matter (F(1,6) = 1, p = 3.599e-12, Table 10). However, it was only the case for chimpanzees as female chimpanzees exhibited higher GA rates than male chimpanzees (est = 0.2397, SE = 0.0255, p < .0001, Table 11) but no difference was found for bonobos.

Rates of yawning did not differ significantly between sexes in a species specific matter (F(1,6) = 1, p = 0.9157, Table 10). However, rates of yawning differed significantly between species (Fig.4) and between sexes (F(1,6) = 1, p = 9.284e-05, Fig.8, Table 12). Chimpanzees showed higher levels of yawning than bonobos do (Fig.4) and males had higher levels of yawning than females did (est = 0.2161, p = 8.58e-05, Fig. 8).

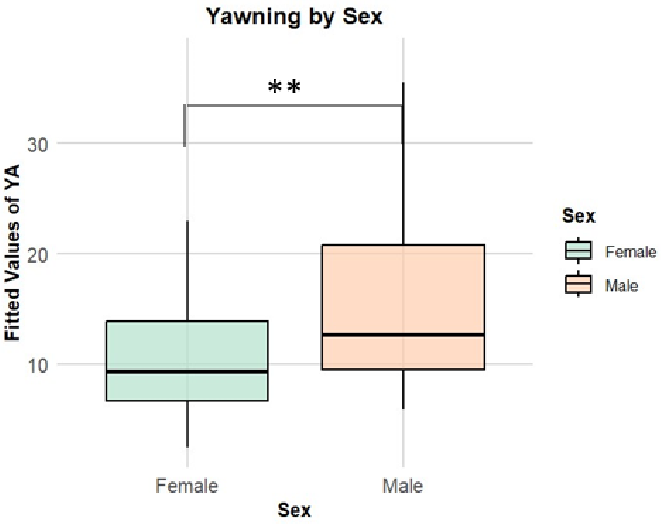


Fig. 8: Comparison of the fitted values of yawning by sex. The x-axis represents the sex (female and male) while the y-axis represents the fitted values of yawning (YA).

The full model (AIC = 1053.470) was not a better fit than the null model (AIC = 1047.208), indicating that rates of nose wiping (NW) did not differ significantly between sexes in a species-specific matter (F(1,6) = 1, p = 0.8275, Table 10). When looking at the effect of the variables species and sex separately, we see that neither species nor sex significantly influenced the rates of nose wiping (species: F(1,6) = 1, p = 0.8656, sex: F(1,6) = 1, p = 0.6043).

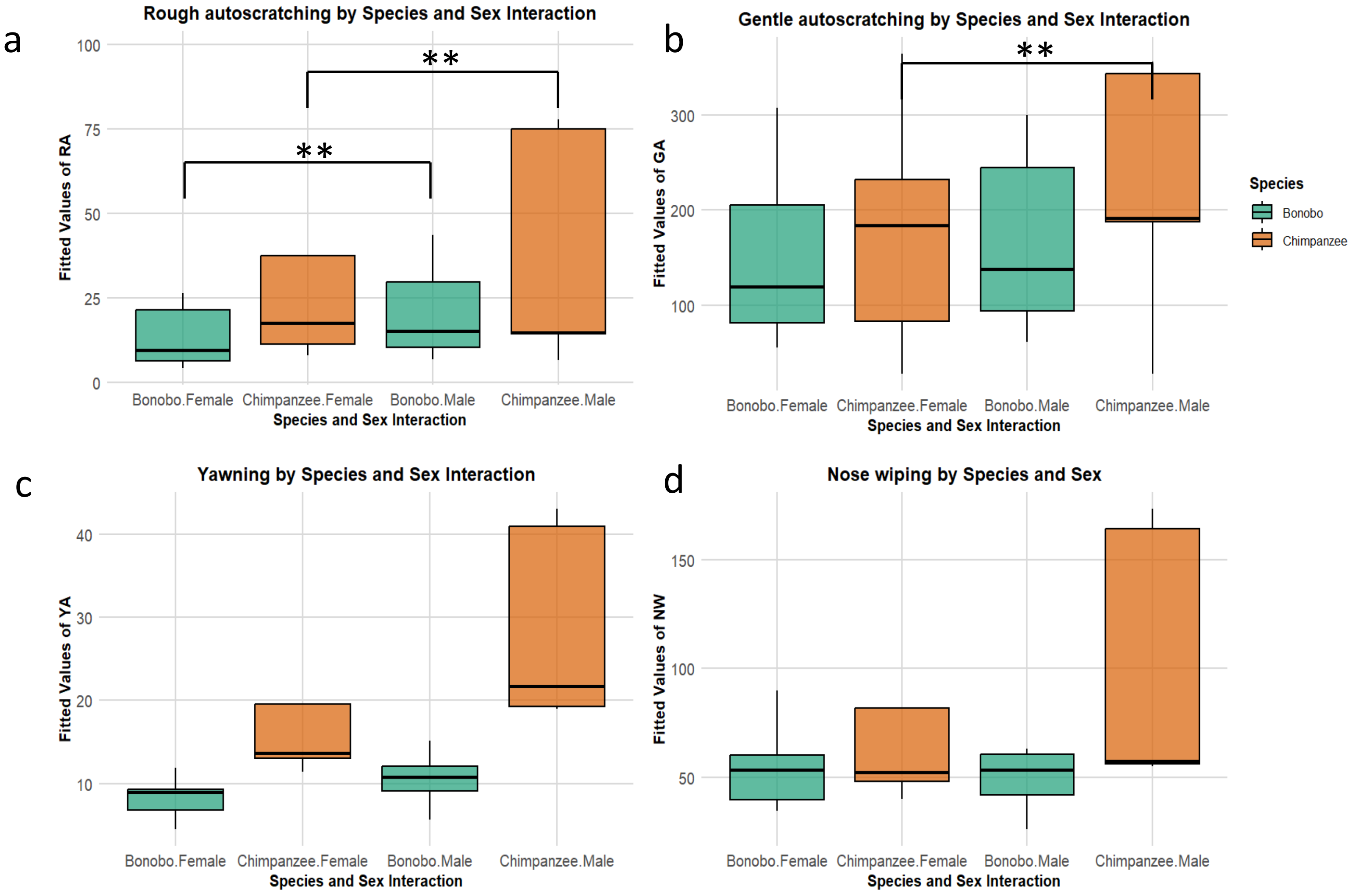


Fig.9. Comparison of the fitted values of the different displacement activities by the interaction of species and sex. The x-axis represents the interaction of the variables species and sex while the y-axis represents the fitted values of each displacement activity. A) rough self-scratching, b) gentle self-scratching, c) nose wiping, d) yawning

3.3.2 *Effect of aggression received*

The amount of aggression an individual received did not increase the rates of either rough autoscratching (RA), yawning (YA) and nose wiping (NW) (RA: F(1,6) = 1, p = 0.5422; YA: F(1,6) = 1, p = 0.1986; NW: F(1,6) = 1, p = 0.2127, Fig.10, Table 10) but it did increase those of gentle autoscratching (est = 0.0020, SE = 0.0005; p < 0.0001, Fig.10, Table 10).

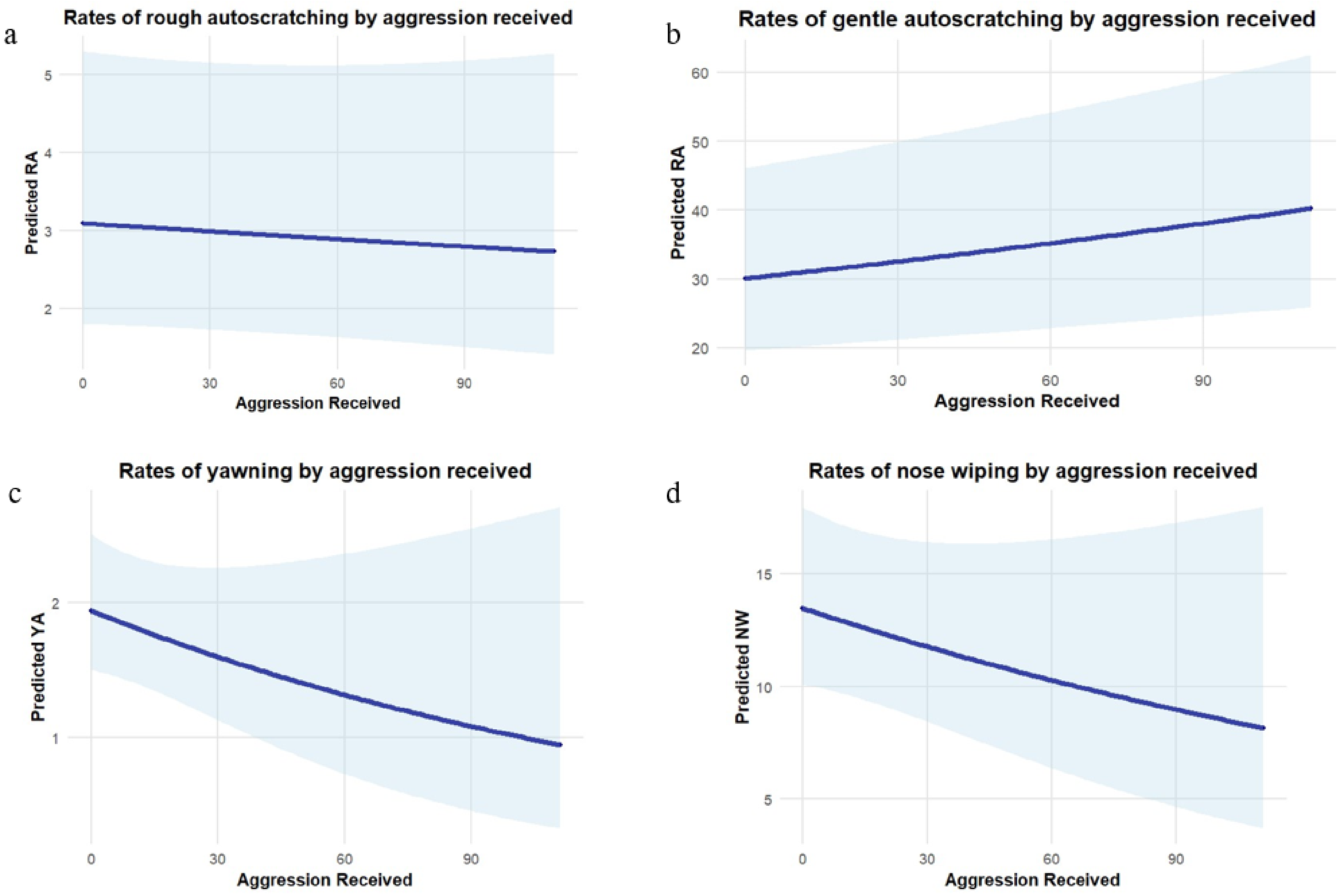


Fig.10: Association between the aggression an individual received and the predicted measures of the different displacement activities. A) rough autoscratching, b) gentle autoscratching, c) yawning, d) nose wiping.

3.3.3 Effect of age

Rates of rough autoscratching (F(1,6) = 1; p = 0.0002, Fig. 11, Table 10), gentle autoscratching (F(1,6) = 1; p = 9.989e-09, Fig. 11, Table 10) and yawning (F(1,6) = 1; p = 0.0015, Fig. 11, Table 10) significantly decreased with the age of an individual. However, age did not have a significant effect on the rates of nose wiping (F(1,6) = 1; p = 0.1464, Fig. 11, Table 10).

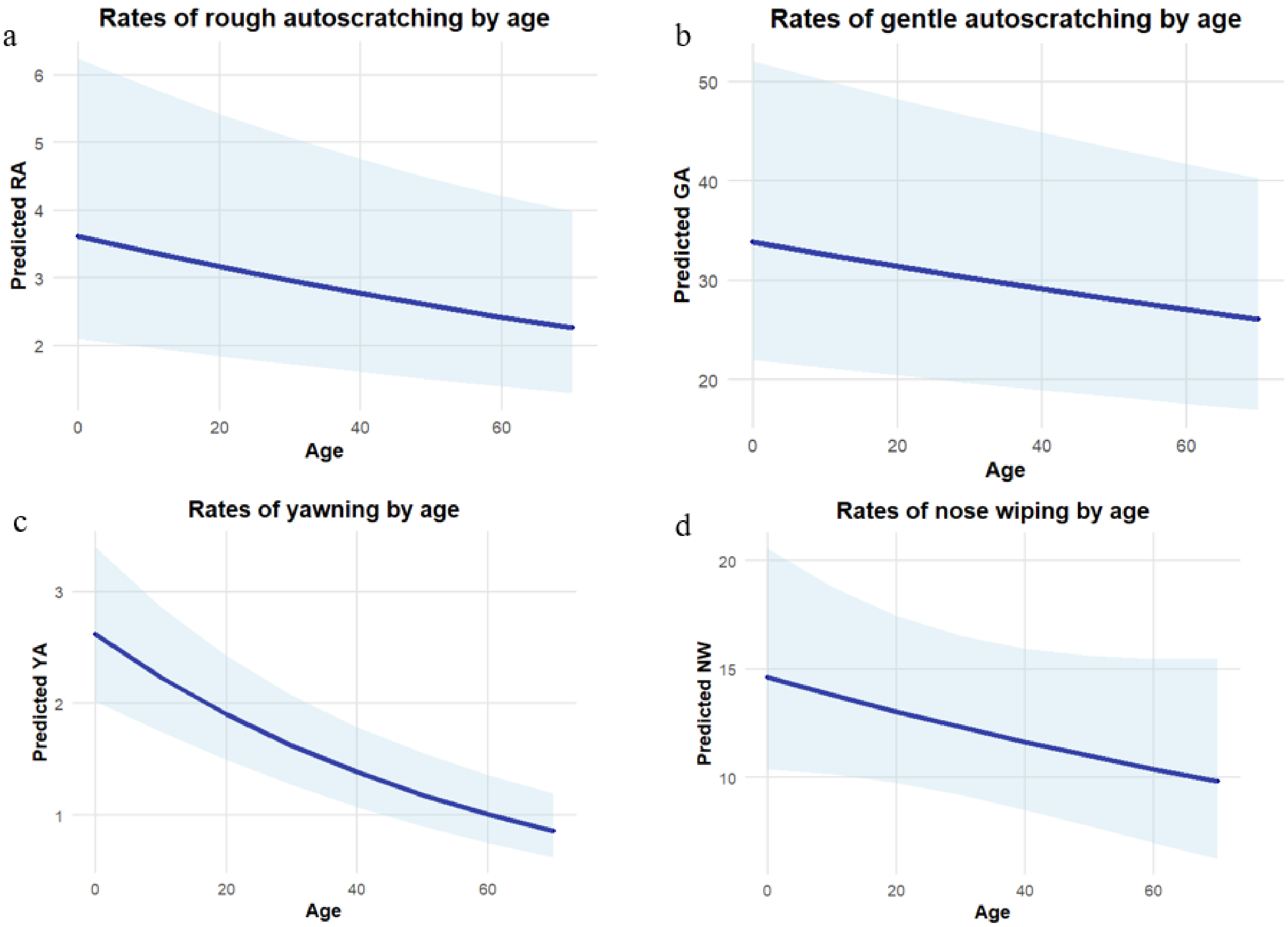


Fig.11. Association between the age of an individual and the predicted measures of the different displacement activities.

Table 10: Results of the drop1 test of the general linear mixed models investigating the effect of the interaction of sex and species, aggression received and age in the rates of displacement behaviors in chimpanzees and bonobos.

Displacement behavior	**Variable**	**Df**	**AIC**	**LRT**	**p-value**
Rough autoscratching	<none>	-	1782.0	-	-
	Age	1	1794.5	14.449	<.0001***
	AggressionReceived	1	1780.4	0.371	0.5422
	Species:Sex	1	1833.9	53.852	<.0001***
Gentle autoscratching	<none>	-	3454.20	-	-
	Age	1	3485.0	32.843	<.0001***
	AggressionReceived	1	3466.4	14.247	0.0002***
	Species:Sex	1	3500.5	48.332	<.0001***
Yawning	<none>	-	749.72	-	-
	Age	1	757.77	10.0487	0.0015**
	AggressionReceived	1	749.37	1.6524	0.1986
	Species:Sex	1	747.73	0.0112	0.9157
Nose wiping	<none>	-	1053.5	-	-
	Age	1	1053.6	2.1096	0.1464
	AggressionReceived	1	1053.0	1.5531	0.2127
	Species:Sex	1	1051.5	0.0475	0.8275

Table 11: Results of the emmeans of the general linear mixed models investigating the effect of the interaction of sex and species, in the rates of displacement behaviors in chimpanzees and bonobos.

contrast	**Displacement behavior**	**estimate**	**SE**	**z.ratio**	**p-value**
Bonobo female – chimpanzee female	*Rough autoscratching*	-0.1838	0.4754	-0.387	0.9804
	Gentle autoscratching	0.34299	0.3797	0.903	0.803
	Yawning	-0.638	0.217	-2.943	0.0172
	Nose wiping	0.0565	0.249	0.277	0.9959
Bonobo female – bonobo male	*Rough autoscratching*	-0.4546	0.0619	-7.34	<.0001
	Gentle autoscratching	-0.0092	0.0239	-0.383	0.9808
	Yawning	-0.306	0.227	-1.35	0.5311
	Nose wiping	-0.036	0.157	-0.229	0.9958
Bonobo female – chimpanzee male	*Rough autoscratching*	0.0233	0.4769	0.049	1.000
	Gentle autoscratching	0.5827	0.38	1.533	0.4174
	Yawning	-0.907	0.25	-3.625	0.0016
	Nose wiping	-0.0325	0.267	-0.121	0.9994
Chimpanzee female – bonobo male	*Rough autoscratching*	-02708	0.4759	-0.569	0.9413
	Gentle autoscratching	-0.3521	0.38	-0.927	0.7905
	Yawning	0.331	0.261	1.267	0.5841
	Nose wiping	-0.0924	0.27	-0.342	0.9862
Chimpanzee female – chimpanzee male	*Rough autoscratching*	0.2070	0.058	3.57	0.002
	Gentle autoscratching	0.2397	0.0255	9.4	<.0.0001
	Yawning	-0.27	0.252	-1.07	0.708
	Nose wiping	-0.089	0.178	-0.5	0.9591
Bonobo male – chimpanzee male	*Rough autoscratching*	0.4779	0.4774	1.001	0.7489
	Gentle autoscratching	0.5918	0.3804	1.556	0.4042
	Yawning	-0.601	0.299	-2.006	0.1855
	Nose wiping	0.0035	0.292	0.012	1.000

Table 12: Results of the drop1 test of the general linear mixed model investigating the effect of species, sex and age in the rates of yawning in chimpanzees and bonobos.

Variable	Df	AIC	LRT	p-value
< none >		1210.4		
Species	1	1214.9	6.465	0.011
Sex	1	1223.7	15.277	9.284e-05
Age	1	1256.6	48.234	3.782e-12

4. DISCUSSION

As a systematic comparison between the two species most closely related to humans (chimpanzees and bonobos) remains unexplored, the aim of this study was to compare the rates of four displacement activities—rough autoscratching, gentle autoscratching, yawning, and nose wiping—between these two species, based on behavioral observations of 76 bonobos and 66 chimpanzees housed in 12 different European zoos. Additionally, the study investigated whether those rates varied according to factors such as the zoo of origin, sex, age or the level of aggression experienced by the individuals.

4.1 Do bonobos and chimpanzees differ significantly in their displacement activities?

The first aim was to measure and compare the rates of displacement activities in chimpanzees and bonobos through the construction of a generalized linear model. Contrary to what was predicted by the self-domestication hypothesis, rates of three out of the four displacement activities (rough autoscratching, gentle autoscratching and nose wiping) did not significantly differ in chimpanzees and bonobos (Fig.5). The only displacement behavior that was significantly higher in chimpanzees was yawning, although not all chimpanzee groups showed higher levels of yawning than all bonobo groups (Fig.5 and 7).

Yawning is a well-documented contagious behavior observed across multiple species, both human and non-human (Palagi et al., 2020). This phenomenon has been studied in chimpanzees and bonobos [chimpanzees: (Anderson et al., 2004; Campbell & De Waal, 2011); bonobos: (Demuru & Palagi, 2012; Norscia et al., 2022; Tan et al., 2017)]. Notably, one comparative study examining yawning rates across the four great apes—chimpanzees, bonobos, gorillas, and orangutans—revealed that only chimpanzees demonstrated a significant increase in yawning when exposed to others yawning. This may explain why higher levels of yawning are observed in chimpanzees compared to bonobos (Fig.5).

However, yawning remains a complicated behavior as it does not serve only one function. Indeed, Smith (1999) proposed over 20 hypotheses to explain the function of yawning, though few have been empirically validated. These hypotheses include increasing alertness (Baenninger et al., 1996), reducing social tension within groups (Sauer & Sauer, 1967), and helping to expel potentially infectious substances from the tonsils (McKenzie, 1994). Yawning rates in this study should then be treated cautiously. But then the question also remains whether yawning truly reflects stress in chimpanzees. Contrary to findings by Aureli and de Waal (1997) and Boekhorst et al. (1991), the correlation between scratching behavior (either rough or gentle) and yawning in chimpanzees was low (Fig. 6, Table 4).

In chimpanzees, rough autoscratching and gentle autoscratching were found to be highly correlated (Fig. 6, Table 4), indicating that chimpanzees who engaged in more rough scratching also engaged in more gentle scratching. Additionally, there was a moderate correlation between nose wiping and gentle autoscratching (Fig.6, Table 4), and the correlation between nose wiping and rough autoscratching was very low (Fig.6, Table 4). Previous studies have suggested that gentle autoscratching may indicate lower levels of negative arousal compared to rough autoscratching (Yamanashi & Matsuzawa, 2010), which could imply that nose wiping is also associated with lower negative arousal. Other studies propose that only rough autoscratching reliably reflects negative arousal (Aureli & de Waal, 1999; Baker & Aureli, 1997; Leavens et al., 2004), while gentle autoscratching may not.

In bonobos, displacement behaviors were poorly correlated with one another (Fig. 6, Table 5). Interestingly, Laméris (2022) demonstrated that bonobos exhibited high levels of gentle autoscratching when responding correctly in a test, suggesting that gentle autoscratching might be linked to positive arousal, while nose wiping is associated with low levels of negative arousal. This distinction could explain why there is no correlation between displacement behaviors in bonobos, as they may be tied to different types of arousal.

It is important to note that arousal can be both positive and negative, and it remains unclear whether specific behaviors are exclusively linked to one type of arousal (e.g., rough autoscratching indicating negative arousal in chimpanzees and gentle autoscratching indicating positive arousal in bonobos) or if both behaviors could reflect both types of arousal simultaneously. There could also have individual preferences in the type of displacement behavior used.

In the future, investigating the contextual occurrences of these behaviors (e.g., before or after a conflict, during play, while eating or moving, etc.) would help to determine if they have positive, negative or neutral valence. Also, further studies might need to be careful in selecting the type of displacement behavior used to measure stress.

4.2 Do group differences outweigh species differences?

The second aim of this study was to determine if the group effect was higher than the species effect via a generalized mixed model. Group had a strong effect on the rates of the four displacement behaviors, especially in rough autoscratching, gentle autoscratching and nose wiping where most groups consistently differed from each other (Fig. 7, Table 6-9). This finding is consistent with our second hypothesis, which posits that group dynamics exert a strong influence on displacement behaviors that outcompetes species-wide patterns.

Yawning was the only displacement behavior that differed in a species-specific way (Fig. 5). However, some groups of chimpanzees have similar rates of yawning to some groups of bonobos. Indeed, chimpanzees from Beauval and Bussolengo have similar rates of yawning than bonobos from Ouwehand and chimpanzees from Apenheul and Dierenrijk have similar rates of yawning than bonobos from Stuttgart 3 (Fig.7). Moreover, the post-hoc comparisons show that yawning rates only differed significantly for one dyad (Table 8). The mechanisms underlying the function of yawning in relation to stress remain poorly understood.

Overall, the rates of displacement behaviors appear to be group-dependent and thus population-specific, rather than species-specific (Fig.7). Multiple reasons can cause these differences between groups such as zoo conditions, social cultures, stressors in the group and individuals physiology.

Various zoo conditions have a significant influence on the performance of displacement behaviors in animals, particularly non-human primates. Captive environments, including zoos, are known to evoke abnormal behavior patterns across species, impacting animal welfare in profound ways (Poole & Granli, 2009; Young, 2013). Factors such as unpredictable feeding schedules and the provision of extractive foraging opportunities have been found to reduce the expression of abnormal behaviors in chimpanzees (Bloomsmith, 1995). Additionally, the availability and quality of enrichment, the type and frequency of food provided, and the size of enclosures are critical in determining stress levels and overall well-being. In a group of bonobos, cortisol levels were higher when food access was restricted (Hohmann, 2009). Access to outdoor spaces (see paragraph below), combined with the presence, quantity, and behavior of zoo visitors, further affects displacement activities, with increased visitor traffic often correlating with elevated anxiety and alterations in natural behaviors, such as yawning in chimpanzees (Baker & Aureli, 1997).

Social culture, defined as "those group-typical behavior patterns shared by members of a community that rely on socially learned and transmitted information" (Laland & Hoppitt, 2003), exhibits remarkable complexity and variation across different primate groups, reflecting their adaptive behaviors and social dynamics. Both chimpanzees and bonobos have long been recognized for their distinct cultural practices [chimpanzees: (Boesch & Boesch, 1990; Goodall, 1986), bonobos: (Hohmann & Fruth, 2003)]. Among chimpanzees, tool-related behaviors dominate cultural expressions, such as the well-known nut-cracking behavior observed in western African populations (Boesch, 1994) and ant-dipping, where sticks are used to extract ants from nests (Boesch & Boesch, 1990; Goodall, 1986). However, social learning also extends beyond tool use. For example, a chimpanzee population utilizes buttressed trees for communication (Boesch, 1991). In bonobos, the social scratch behavior is similarly transmitted through social learning (van Leeuwen et al., 2020). Displacement behaviors could also be socially transmitted, with their transmission varying between groups, potentially explaining the observed differences in the frequency of these behaviors across the different groups. Social culture may sometimes be transmitted more through kinship, as genetic predispositions can influence an individual's likelihood of acquiring certain behaviors, such as the groom-slap behavior observed in bonobos (van Leeuwen et al., 2020). Although our study did not test for kinship effects, future research could explore this possibility.

High-density conditions and crowding can significantly influence the rates of displacement behaviors in primates. In chimpanzees, crowding within their group has been linked to increased rates of behaviors such as scratching and yawning, particularly in conditions where space is limited (Aureli & de Waal, 1997). Lack of access to outdoor enclosures exacerbates this stress, as decreased available surface area elevates the rates of displacement behaviors (Aureli & de Waal, 1997). However, this theory has been challenged by a study that found higher rates of self-directed behaviors, including autoscratching, when chimpanzees had access to outdoor spaces (Bonnie, 2016). Despite this contradiction, it is clear that outdoor access has an effect on displacement behaviors like yawning and scratching. Although no studies have directly addressed the impact of crowding on displacement behaviors in bonobos, research suggests they employ similar tension-reduction strategies to chimpanzees under high-density conditions (Videan & Fritz, 2007), indicating that comparable outcomes could be expected. However, further research is needed to draw definitive conclusions. Here, there was insufficient variation to analyze outdoor access in relation to different seasons. However, it is worth noting that the Antwerp group, which exhibited some of the highest rates of displacement behaviors, did not always have access to their outdoor enclosure during observations, as these were conducted in the winter months.

Individual physiological differences within a group can significantly impact behavior, roles, and social interactions, shaping the dynamics of the entire group. Variations in size, strength, hormonal levels, and metabolic rates all contribute to individual responses to environmental and social stimuli. For example, dominant chimpanzees exhibit higher testosterone levels, which increase aggression and can affect both their own stress levels and those of their group members (Wobber et al., 2010). Additionally, genetic variations, such as mutations in the serotonin receptor gene, can make some individuals more or less sensitive to serotonin. While bonobos have more serotonin transporters in their amygdala than chimpanzees (Hare, 2012; Staes et al., 2019), studies in chimpanzees reveal that individuals with ancestral alleles in their serotonin receptor gene show higher scratching rates compared to those without (Staes et al., 2019). This individual variation in serotonin levels can influence the rates of displacement behaviors, which in turn affects the overall behavior patterns of the group.

Variations in dominance hierarchy and its stability may significantly influence the rates of displacement behaviors across different groups. Research on baboons has shown a correlation between dominance instability and elevated cortisol levels in both high- and low-ranking males, whereas periods of dominance stability were associated with the opposite effect (Sapolsky, 2005). In chimpanzees, while aggression received appears to have a more pronounced effect on glucocorticoid levels than rank itself (Muller et al., 2021), fluctuations in hierarchy stability across groups could explain observed differences in the frequency of displacement behaviors. The variation in dominance stability may thus contribute to the overall stress levels within groups, driving differences in how frequently these behaviors are expressed.

Multiple additional social stressors within groups can contribute to variations in displacement behaviors. For instance, in the Antwerp group, individuals were split into two separate groups for breeding purposes during observations, potentially elevating stress levels in some members. Similarly, in the Beauval group, ongoing work in one of the chimpanzee enclosures forced all individuals into a single space, creating high-density conditions. The accompanying noise and disturbances from workers, particularly from tools like screw guns and welding machines, led to heightened stress, as evidenced by frequent vocalizations such as alarm calls and screams, as well as indirect displays of distress (personal observations). These environmental and social stressors likely exacerbated anxiety and contributed to induce variations of stress levels in the different groups.

The Antwerp group emerged as an outlier, exhibiting the highest rates displacement behaviors across all measured categories (Fig.7). During the time of observation, this group was separated into two subgroups for breeding purpose. One female in particular appeared notably anxious due to the separation from her sister, with whom she shared a close bond, and faced challenges integrating into the breeding subgroup. This highlights the significant role social climate within a group plays in influencing rates of displacement behaviors.

It underscores the need to consider the impact of group dynamics, such as social bonds and subgrouping, when analyzing stress-related behaviors. Numerous factors can cause variations in displacement behaviors in bonobos and chimpanzees, with social stressors, environmental changes, and group dynamics playing significant roles. In this study, we focused on analyzing the effects of three key factors: aggression received, age, and sex, to better understand their influence on displacement behaviors.

4.3 What factors explain displacement activities variation in Pan?

The third aim of this study was to identify underlying factors that influence variations in displacement behaviors at an individual level like sex, age and aggression received through a generalized mixed model.

4.3.1 Effect of the interaction between sex and species

Rates of displacement activities differed significantly between sexes in a species-specific manner for the scratching behavior only with male bonobos displaying higher rates of rough autoscratching than female bonobos while female chimpanzees displayed higher rates than male chimpanzees (Fig.9, Table 11). Female chimpanzees also displayed higher rates of gentle autoscratching than male chimpanzees but no significant difference was found for bonobos (Fig.9, Table 11). This is in alignment with our finding of the correlation between rough autoscratching and gentle autoscratching in chimpanzees and the fact that this correlation does not exist in bonobos (Fig. 6, Tables 4 and 5). The findings of our study contrast with those of Hopkins (2006), who reported no significant sex differences in rates of self-directed behaviors among chimpanzees in an experimental setting. However, supporting evidence from Baker and Aureli (1997) suggests that female chimpanzees exhibit increased rates of rough autoscratching when in the proximity of group members, a pattern not observed in males. This sex difference in self-directed behaviors is further supported by research on other primates. High levels of self-directed behaviors, including rough autoscratching, have been documented among subordinate individuals in both baboon (Easley et al., 1987) and long-tailed macaque groups (Pavani et al., 1991). Notably, subordinates in chimpanzee societies tend to be females, while in bonobos, subordinates are typically males. These distinctions align with the patterns observed in our results, suggesting that social status and sex may play a key role in shaping displacement activities across primate species.

Female chimpanzees exhibited higher rates of gentle autoscratching compared to males (Fig. 9, Table 11), a behavior that may indicate uncertainty during interactions among group members (Aureli & de Waal, 1997). This heightened rate in females could be linked to the fact that female chimpanzees tend to be less socially bonded with one another and with males compared to the stronger bonds observed among male chimpanzees. This weaker social connection could lead to increased relationship distress, manifesting as higher gentle autoscratching. In contrast, no significant differences in gentle autoscratching were observed between male and female bonobos (Fig. 9, Table 11), a species known for closer social bonds, particularly between females and between males and their mothers. This pattern further supports the idea that the frequency of gentle autoscratching may be influenced by the strength of social relationships within the group.

This interaction effect between sex and species further refines our findings regarding species differences, where chimpanzees exhibited higher yawning rates than bonobos (Fig. 4). Specifically, female bonobos, unlike males, showed significantly lower yawning rates compared to both male and female chimpanzees (Table 12).

Neither species nor sex nor the interaction between the two significantly influenced the rates of nose wiping. This means that nose wiping is neither sex nor species dependent and that its rates depend on other factors.

4.3.2 Effect of aggression received

The amount of aggression an individual received only had a positive association with one displacement behavior, as rates of gentle autoscratching increased with the rates of aggression an individual received (Fig. 10, Table 10). Although the results were not statistically significant, we observed a pattern suggesting that rates of displacement behaviors, with the exception of gentle autoscratching, tended to decrease as the level of aggression an individual experienced increased (Fig. 10). This observation implies that different displacement behaviors may reflect varying degrees or types of emotional arousal, possibly distinguishing between negative and positive states. However, previous studies found that rough autoscratching is a more reliable of anxiety than gentle autoscratching (Aureli & de Waal, 1999; Baker & Aureli, 1997), and it tends to be displayed more rapidly (Leavens et al., 2004). This could mean that aggression received does not have the effect intended or that additional factors need to be considered, such as the context in which the behavior is displayed.

Individuals may exhibit a preference for specific self-directed behaviors (SDBs) depending on the context of the stress they encounter. Context, whether it involves social tension, aggression, or cognitive stress, can profoundly influence the type of SDBs displayed. For instance, chimpanzees tend to engage in higher levels of self-scratching and yawning during periods of social tension or anxiety (Baker & Aureli, 1997), whereas bonobos yawn less in the immediate aftermath of social stress (Demuru & Palagi, 2012). Additionally, bonobos are more likely to exhibit nose wiping in response to frustration during cognitive testing (Kret et al., 2016). In the wild, contextual nuances also affect these behaviors, as Arnold and Whiten (2001) found that gentle and rough autoscratching in chimpanzees did not increase following aggression, and that scratching rates were lower after reconciled conflicts compared to unreconciled ones. The context of aggression may therefore play a key role in interpreting the observed rates of displacement behaviors.

4.3.3 Effect of age

The rates of displacement behaviors decreased as an individual (whether bonobo or chimpanzee) aged, except for nose wiping (Fig. 11, Table 10). This trends aligns with a study that shows that peak cortisol levels occurred earlier and baseline cortisol levels were higher in younger chimpanzees compared to older ones, suggesting a link between age and stress physiology (Anestis et al., 2006). Other studies found an opposite pattern, with stress hormone levels increasing with age (M. E. Thompson, 2010). Notably, Thompson's study focused exclusively on reproductive female chimpanzees, a group we did not analyze separately here. Additionally, cortisol alone cannot fully capture stress levels, particularly since it tends to show an age-related decline. In humans, it is shown that circadian cortisol rhythms and hypothalamic–pituitary–adrenal (HPA) axis feedback mechanisms are altered with aging (O'Brien et al., 1994; Sharma et al., 1989; Sherman et al., 1985; Van Cauter et al., 1996).

Another study found that there were no significant differences in scratching and yawning rates between younger (11-22 years) and older (30-44 years) chimpanzees (Baker, 2000). Although this study does not capture the full range of age-related variability, it highlights the importance of dividing into age groups rather than treating age as a linear variable, which is the method we employed in our analysis.

The decrease of rates of displacement behaviors with age can mean that older individuals better learn to cope with stress than younger ones. In savannah baboons (*Papio sp.*), for instance, the relation an individual had with its mother can play an important role in the way they cope with stress as an adult; if the mother is stressed, their juveniles can be stressed as well (Bardi et al., 2005). Similarly, in Japanese macaques (*Macaca fuscata*), offspring of more rejecting mothers become independent at an earlier age and cope better with social stressors as adults (Bardi & Huffman, 2002; Schino et al., 2001). Infants, however, may be less affected by stressors within the group due to the protective effects of affiliative maternal behaviors, which can buffer them from these stressors (Stanton et al., 2015). This highlights the importance of considering age groups rather than treating age as a linear factor, as well as examining the interaction of multiple factors rather than isolating one.

4.4 Limitations of the study

The function of yawning is still poorly understood. No distinction between yawns related to drowsiness and sleepiness (rest yawns) and tension or aggressive yawns (Deputte, 1994; Maestripieri, 1992) was made. Yawning is a behavior long known in the repertoire of primates (Darwin, 1867). Wild chimpanzees, for example, are reported to yawn more in response to human proximity (Goodall, 1986; Nishida, 1970), while increased yawning was found in response to social tension in captive chimpanzees (Baker & Aureli, 1997). Plus, some yawns are contagious (in chimpanzees: (Anderson et al., 2001; Campbell et al, 2009), in bonobos: Norscia, 2022) so we cannot be sure that yawning rates are only due to stress as we did not distinguish between rest yawns and tension yawn. Yet, in captive chimpanzees, one study found that nearly all instances of yawning (98.2%) occurred during periods of rest while sitting and lying down (Vick & Paukner, 2010).

A notable limitation of this study is that displacement behaviors were analyzed independently of the surrounding actions or events, without considering critical contextual factors such as levels of aggression or potential social contagion. Previous research has shown that displacement behavior rates, like rough autoscratching, vary significantly depending on the activity the focal individual is engaged in. For example, rates of rough autoscratching are low during foraging and movement but increase during resting and socializing (Kutsukake, 2003). As highlighted in our earlier discussion of aggression, context is crucial in interpreting these behaviors. Additionally, social contagion may influence displacement behaviors. For instance, chimpanzees exhibit increased self-directed behaviors when exposed to social interactions on a computer monitor, suggesting the contagion of arousal (Hopkins, 2006). A similar effect has been observed in Japanese macaques (*Macaca fuscata*) (Nakayam, 2004). Therefore, the omission of contextual elements such as social dynamics and individual activities limits the comprehensiveness of our findings.

5. CONCLUSION

The primary objective of this study was to compare the rates of four displacement behaviors – rough autoscratching, gentle autoscratching, yawning and nose wiping – between chimpanzees (*Pan troglodytes*) and bonobos (*Pan paniscus*) to further look into the differences and resemblances of these two species. It has been revealed that, contrary to initial expectations, the stress responses between these two species are relatively similar. Notably, the variability in displacement behaviors was more pronounced within groups than between species (with the exception of yawning), indicating that environmental and social factors play a more critical role in shaping these behaviors than phylogenetic differences. Factors such as zoo housing conditions, crowding, access to outdoor enclosures, and group dynamics appear to strongly influence the rates of displacement behaviors. Additionally, individual characteristics such as sex and age contribute to this variability, with female chimpanzees exhibiting higher levels of autoscratching than males, and male bonobos showing more gentle autoscratching than females. These findings point to different selection pressures linked to the distinct social structures of chimpanzees and bonobos, with chimpanzees exhibiting more male-dominated societies and bonobos emphasizing female bonding. Interestingly, older individuals in both species demonstrated fewer displacement behaviors, suggesting improved stress management with age, although the relationship between age and stress warrants further investigation. This study also underlines the complexity of interpreting displacement behaviors, as aggression received was associated with a decrease in gentle autoscratching, underscoring the importance of context. The low correlation rates between displacement behaviors in both species (with the exception of rough and gentle autoscratching in chimpanzees) suggests that these behaviors might be used as different functions and indicating different levels or intensity of arousal. This study revealed that only one factor, the individual's group, influenced nose wiping rates, highlighting the need for further research to gain a deeper understanding of what affects this behavior. Additionally, the limitations in understanding the various functions of yawning and the lack of contextual information surrounding displacement behaviors underscores the need for further research. In the future, adopting a more holistic approach that incorporates multiple interacting factors is then essential to deepen our understanding of the mechanisms underlying displacement behaviors and achieve more accurate interpretations of stress responses across the *Pan* genus.

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7. ANNEXES

Annex 1: Chimpanzees included in this study and their respective zoos, their sex, their birthdate and the period during which they were observed.

Zoo	Name	Sex	Age at the beginning of the study	Observation period
Antwerp	Arnold	M	45.09	2023
	Tuma	M	30.16	
	Tambuzi	M	30.25	
	Chita	M	41.09	
	Jamie	M	33.13	
	Siri	F	31.32	
	Marit	F	17.02	
	Kitoto	F	39.24	
	Lomela	F	33.76	
	Nancy	F	44.08	
	Mia	F	14.41	
Beauval	Gypso	F	37.03	2024
	Joseph	M	49.19	
	Yumbi	M	10.06	
	Domi	F	34.25	
	Lukombe	M	12.58	
	Julie	F	41.77	
	Micheline	F	34.13	
	Charlotte	F	47.52	
	Tumba	M	15.13	
	N’Sàka	M	2.77	
	Bonobo	F	41.77	
	Wamba	F	15.27	
	Lobaï	M	9.72	

	Sangha	F	17.61	
Dierenrijk	Pat	M	24.08	2023
	Fahamu	M	15.12	
	Christa	F	35.74	
	Kibibi	F	6.95	
	Jana	F	37.74	
	Jozie	F	13.25	
	Sonja	F	56.78	
	Kymani	F	0.62	
Bussolengo	Mary	f	33.97	2024
	Madax	F	14	
	Giorgina	F	21.67	
	Sammy	F	52.11	
	Valentina	F	17.96	
	Giuditta	F	18.1	
	Tommy	M	27.01	

Annex 2: Bonobos included in this study and their respective zoos, their sex, their birthdate and the period during which they were observed.

Zoo	Name	Sex	Age at the beginning of the study	Observation period
Apenheul	Ayebi	F	7.2	2022
	Besede	F	16.2	
	Bolombe	M	24.3	
	Bonnie	F	45.9	
	Eyenga	M	4.0	
	Jill	F	36.6	
	Kindu	M	37.4	
	Kumbuka	F	22.6	
	Lokolo	M	3.7	
	Makasi II	M	12.5	
	Neje	F	1.0	
	Pangi	F	12.6	
Frankfurt	Bashira	F	16.3	2022
	Bokati	M	1.3	
	Boni	M	1.3	
	Hanna	F	14.5	
	Heri	M	21.4	
	Kamiti	F	35.4	
	Margrit	F	70.6	
	Mixi	F	20.5	
	Natalie	F	57.5	
	Nayoki	F	10.2	
	Nyota II	M	15.3	
	Panisco	M	12.5	
	Sambo	M	10.4	
	Xekele	F	4.4	
	Xola	F	5.2	
	Yango	M	4.1	
	Zomi I	F	24.3	
Ouwehand	Ayubu	M	10.7	2022
	Azibo	M	10.7	

	Bakari	M	4.8	
	Bondo	M	30.6	
	Eja	F	31.8	
	Kutu	F	23.9	
	Lingoye	F	14.4	
	Lisala	F	42.0	
	Luebo	M	16.1	
	Maiyko	M	2.4	
	Mmbe	M	0.1	
	Nginga	F	3.7	
	Omanga	F	13.3	
	Visola	F	6.7	
Planckendael : summer	Banya	F	31.6	2021
	Binti	F	26.0	
	Busira	F	17.5	
	Djanoa	F	26.4	
	Habari	M	15.6	
	Hortense	F	43.2	
	Kianga	F	16.1	
	Kikongo	M	7.6	
	Mokonzi	M	8.5	
	Nayembi	F	15.3	
	Vifijo	M	27.1	
	Zamba	M	23.4	
	Balina	F	1.7	
	Bina	F	6.4	
	Moko II	M	5.5	
	Nila	F	6.0	
	Sanza	F	4.5	

	Unabii	F	1.6	
	Vyombo	M	0.8	
	Wakati	F	0.6	
Planckendael : winter	Balina	F	1.1	2021
	Banya	F	31.0	
	Bina	F	5.8	
	Binti	F	25.4	
	Busira	F	16.9	
	Djanoa	F	25.8	
	Habari	M	15.0	
	Hortense	F	42.6	
	Kianga	F	15.5	
	Kikongo	M	7.0	
	Moko II	M	4.9	
	Mokonzi	M	7.9	
	Nayembi	F	14.7	
	Nila	F	5.4	
	Sanza	F	4.0	
	Unabii	F	1.0	
	Vifijo	M	26.5	
	Vyombo	M	0.2	
	Wakati	F	0.0	
	Zamba	M	22.8	
Stuttgart 1	Chipita	F	28.5	2022
	Haiba	F	20.3	
	Kasai I	M	17.2	
	Kenai	M	1.8	
	Kolela	F	6.0	
	Liboso	F	24.2	

	Lubao	M	8.9	
	Nio	M	2.5	
Stuttgart 2	Bikita	F	11.7	2022
	Bobali	M	8.7	
	Huenda	F	15.7	
	Kombote	F	55.3	
	Lukombo	M	0.7	
	Makasi III	M	6.3	
	Malua	F	0.0	
	Mary Rose	F	12.0	
	Xhosa	M	4.2	
Stuttgart 3	Banbo	F	19.5	2022
	Chimba	F	27.2	
	Kaju	M	4.2	
	Mobikisi	M	41.7	
	Omari	M	0.0	
	Yanola	F	6.1	
Vallée des Singes	Daniela	F	53.4	2021
	David	M	20.3	
	Diwani	M	25.2	
	Kelele	M	17.3	
	Khalessi	F	8.9	
	Khaya	F	20.1	
	Kymia II	F	4.5	
	Lingala	F	18.3	
	Lokoro	M	6.4	
	Loto	M	12.2	
	Lucy II	F	17.9	
	Moko I	M	9.3	

	Swahili	F	7.1	
	Ukela	F	35.9	
	Ulindi	F	28.1	
	Yahimba	F	12.2	
	Yuli	F	7.3	

Annex 3: Results of the drop1 test of the general linear mixed models investigating the species effect in the rates of displacement behaviors in chimpanzees and bonobos.

Displacement behavior	**Variable**	**Df**	**AIC**	**LRT**	**p-value**
Rough autoscratching	<none>	-	1863.8	-	-
	Species	1	1861.9	0.0585	0.8089
Gentle autoscratching	<none>	-	3614.0	-	-
	Species	1	3613.3	1.3891	0.2386
Yawning	<none>	-	755.65	-	-
	Species	1	759.23	5.5711	0.0183*
Nose wiping	<none>	-	1049.2	-	-
	Species	1	1047.2	0.0277	0.8678

Annex 4: Results of the drop1 test of the general linear mixed models investigating the group effect in the rates of displacement behaviors in chimpanzees and bonobos.

Displacement behavior	**Variable**	**Df**	**AIC**	**LRT**	**p-value**
Rough autoscratching	<none>	-	816.86	-	-
	Group	11	905.67	112.81	<2.2e-16***
Gentle autoscratching	<none>	-	1177.8	-	-
	Group	11	1278.7	122.96	<2.2e-16***
Yawning	<none>	-	757.24	-	-

	Group	11	762.40	27.156	0.0044**
Nose wiping	<none>	-	1036.5	-	-
	Group	11	1069.1	54.667	8.916e-08***

Annex 5: Table of dyadic significance between groups for RA

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Pair of groups                        estimate    SE  df z.ratio p.value
 Antwerp - Apenheul                     0.5445 0.313 Inf   1.740  0.8497
 Antwerp - Beauval                      1.0284 0.288 Inf   3.565  0.0188
 Antwerp - Bussolengo                   2.3300 0.357 Inf   6.525  <.0001
 Antwerp - Dierenrijk                   1.6250 0.367 Inf   4.431  0.0006
 Antwerp - Frankfurt                    1.6547 0.299 Inf   5.533  <.0001
 Antwerp - Ouwehand                     2.3609 0.330 Inf   7.144  <.0001
 Antwerp - Planckendael_Winter          1.2751 0.295 Inf   4.320  0.0009
 Antwerp - Stuttgart1                   0.8047 0.379 Inf   2.121  0.6079
 Antwerp - Stuttgart2                   0.3388 0.378 Inf   0.896  0.9992
 Antwerp - Stuttgart3                   0.3756 0.455 Inf   0.825  0.9996
 Antwerp - ValleeDesSinges              1.6435 0.288 Inf   5.713  <.0001
 Apenheul - Beauval                     0.4839 0.308 Inf   1.569  0.9202
 Apenheul - Bussolengo                  1.7855 0.373 Inf   4.783  0.0001
 Apenheul - Dierenrijk                  1.0805 0.383 Inf   2.824  0.1695
 Apenheul - Frankfurt                   1.1103 0.318 Inf   3.488  0.0245
 Apenheul - Ouwehand                    1.8164 0.348 Inf   5.220  <.0001
 Apenheul - Planckendael_Winter         0.7306 0.315 Inf   2.322  0.4606
 Apenheul - Stuttgart1                  0.2602 0.395 Inf   0.659  1.0000
 Apenheul - Stuttgart2                 -0.2057 0.394 Inf  -0.523  1.0000
 Apenheul - Stuttgart3                 -0.1688 0.468 Inf  -0.361  1.0000
 Apenheul - ValleeDesSinges             1.0990 0.308 Inf   3.573  0.0183
 Beauval - Bussolengo                   1.3016 0.353 Inf   3.686  0.0122
 Beauval - Dierenrijk                   0.5966 0.363 Inf   1.644  0.8927
 Beauval - Frankfurt                    0.6263 0.294 Inf   2.128  0.6024
 Beauval - Ouwehand                     1.3325 0.326 Inf   4.086  0.0026
 Beauval - Planckendael_Winter          0.2467 0.290 Inf   0.850  0.9995
 Beauval - Stuttgart1                  -0.2237 0.376 Inf  -0.595  1.0000
 Beauval - Stuttgart2                  -0.6896 0.374 Inf  -1.842  0.7947
 Beauval - Stuttgart3                  -0.6528 0.452 Inf  -1.443  0.9549
 Beauval - ValleeDesSinges              0.6151 0.283 Inf   2.176  0.5675
 Bussolengo - Dierenrijk               -0.7050 0.419 Inf  -1.681  0.8773
 Bussolengo - Frankfurt                -0.6752 0.362 Inf  -1.866  0.7803
 Bussolengo - Ouwehand                  0.0309 0.388 Inf   0.080  1.0000
 Bussolengo - Planckendael_Winter      -1.0549 0.359 Inf  -2.942  0.1264
 Bussolengo - Stuttgart1               -1.5253 0.431 Inf  -3.542  0.0204
 Bussolengo - Stuttgart2               -1.9912 0.430 Inf  -4.636  0.0002
 Bussolengo - Stuttgart3               -1.9543 0.499 Inf  -3.918  0.0051
 Bussolengo - ValleeDesSinges          -0.6865 0.352 Inf  -1.948  0.7289
 Dierenrijk - Frankfurt                 0.0297 0.371 Inf   0.080  1.0000
 Dierenrijk - Ouwehand                  0.7359 0.397 Inf   1.853  0.7880
 Dierenrijk - Planckendael_Winter      -0.3499 0.368 Inf  -0.950  0.9986
 Dierenrijk - Stuttgart1               -0.8203 0.439 Inf  -1.870  0.7781
 Dierenrijk - Stuttgart2               -1.2862 0.438 Inf  -2.940  0.1271
 Dierenrijk - Stuttgart3               -1.2494 0.506 Inf  -2.470  0.3588
 Dierenrijk - ValleeDesSinges           0.0185 0.362 Inf   0.051  1.0000
 Frankfurt - Ouwehand                   0.7062 0.336 Inf   2.104  0.6197
 Frankfurt - Planckendael_Winter       -0.3797 0.301 Inf  -1.262  0.9836
 Frankfurt - Stuttgart1                -0.8501 0.384 Inf  -2.214  0.5392
 Frankfurt - Stuttgart2                -1.3160 0.383 Inf  -3.439  0.0289
 Frankfurt - Stuttgart3                -1.2791 0.459 Inf  -2.786  0.1857
 Frankfurt - ValleeDesSinges           -0.0112 0.294 Inf  -0.038  1.0000
 Ouwehand - Planckendael_Winter        -1.0858 0.332 Inf  -3.270  0.0498
 Ouwehand - Stuttgart1                 -1.5562 0.409 Inf  -3.806  0.0078
 Ouwehand - Stuttgart2                 -2.0221 0.408 Inf  -4.961  <.0001
 Ouwehand - Stuttgart3                 -1.9853 0.480 Inf  -4.135  0.0021
```

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 Ouwehand - ValleeDesSinges           -0.7174 0.325 Inf  -2.204  0.5464
 Planckendael_Winter - Stuttgart1     -0.4704 0.381 Inf  -1.235  0.9862
 Planckendael_Winter - Stuttgart2     -0.9363 0.380 Inf  -2.467  0.3612
 Planckendael_Winter - Stuttgart3     -0.8995 0.457 Inf  -1.970  0.7140
 Planckendael_Winter - ValleeDesSinges  0.3684 0.290 Inf   1.272  0.9825
 Stuttgart1 - Stuttgart2              -0.4659 0.448 Inf  -1.039  0.9968
 Stuttgart1 - Stuttgart3              -0.4290 0.515 Inf  -0.833  0.9996
 Stuttgart1 - ValleeDesSinges          0.8388 0.375 Inf   2.236  0.5229
 Stuttgart2 - Stuttgart3               0.0369 0.514 Inf   0.072  1.0000
 Stuttgart2 - ValleeDesSinges          1.3048 0.374 Inf   3.491  0.0243
 Stuttgart3 - ValleeDesSinges          1.2679 0.452 Inf   2.807  0.1769
```

Annex 6: Table of dyadic significance between groups for GA

```
Pair of groups                       estimate    SE  df z.ratio p.value
 Antwerp - Apenheul                   -0.1107 0.172 Inf  -0.645  1.0000
 Antwerp - Beauval                    -0.0207 0.157 Inf  -0.132  1.0000
 Antwerp - Bussolengo                  1.3279 0.188 Inf   7.082  <.0001
 Antwerp - Dierenrijk                  2.1279 0.207 Inf  10.285  <.0001
 Antwerp - Frankfurt                   0.6807 0.160 Inf   4.242  0.0013
 Antwerp - Ouwehand                   -0.3358 0.166 Inf  -2.017  0.6817
 Antwerp - Planckendael_Winter         0.2946 0.160 Inf   1.843  0.7939
 Antwerp - Stuttgart1                  0.4211 0.207 Inf   2.030  0.6729
 Antwerp - Stuttgart2                  0.5964 0.210 Inf   2.842  0.1624
 Antwerp - Stuttgart3                  0.7193 0.253 Inf   2.839  0.1635
 Antwerp - ValleeDesSinges             0.8704 0.154 Inf   5.658  <.0001
 Apenheul - Beauval                    0.0901 0.166 Inf   0.542  1.0000
 Apenheul - Bussolengo                 1.4387 0.196 Inf   7.356  <.0001
 Apenheul - Dierenrijk                 2.2386 0.214 Inf  10.451  <.0001
 Apenheul - Frankfurt                  0.7914 0.170 Inf   4.660  0.0002
 Apenheul - Ouwehand                  -0.2251 0.175 Inf  -1.283  0.9814
 Apenheul - Planckendael_Winter        0.4053 0.169 Inf   2.396  0.4088
 Apenheul - Stuttgart1                 0.5319 0.215 Inf   2.476  0.3548
 Apenheul - Stuttgart2                 0.7072 0.217 Inf   3.258  0.0516
 Apenheul - Stuttgart3                 0.8300 0.259 Inf   3.200  0.0614
 Apenheul - ValleeDesSinges            0.9811 0.164 Inf   5.998  <.0001
 Beauval - Bussolengo                  1.3486 0.183 Inf   7.387  <.0001
 Beauval - Dierenrijk                  2.1486 0.202 Inf  10.615  <.0001
 Beauval - Frankfurt                   0.7013 0.155 Inf   4.535  0.0004
 Beauval - Ouwehand                   -0.3152 0.161 Inf  -1.959  0.7213
 Beauval - Planckendael_Winter         0.3152 0.154 Inf   2.048  0.6604
 Beauval - Stuttgart1                  0.4418 0.203 Inf   2.176  0.5670
 Beauval - Stuttgart2                  0.6171 0.205 Inf   3.004  0.1073
 Beauval - Stuttgart3                  0.7399 0.250 Inf   2.964  0.1194
 Beauval - ValleeDesSinges             0.8910 0.148 Inf   6.030  <.0001
 Bussolengo - Dierenrijk               0.8000 0.227 Inf   3.521  0.0219
 Bussolengo - Frankfurt               -0.6473 0.186 Inf  -3.481  0.0251
 Bussolengo - Ouwehand                -1.6638 0.191 Inf  -8.705  <.0001
 Bussolengo - Planckendael_Winter     -1.0334 0.185 Inf  -5.575  <.0001
 Bussolengo - Stuttgart1              -0.9068 0.228 Inf  -3.982  0.0039
 Bussolengo - Stuttgart2              -0.7315 0.230 Inf  -3.182  0.0648
 Bussolengo - Stuttgart3              -0.6087 0.270 Inf  -2.253  0.5107
 Bussolengo - ValleeDesSinges         -0.4576 0.180 Inf  -2.539  0.3155
 Dierenrijk - Frankfurt               -1.4472 0.205 Inf  -7.044  <.0001
 Dierenrijk - Ouwehand                -2.4637 0.210 Inf -11.723  <.0001
 Dierenrijk - Planckendael_Winter     -1.8333 0.205 Inf  -8.947  <.0001
 Dierenrijk - Stuttgart1              -1.7068 0.244 Inf  -6.997  <.0001
 Dierenrijk - Stuttgart2              -1.5315 0.246 Inf  -6.227  <.0001
 Dierenrijk - Stuttgart3              -1.4086 0.284 Inf  -4.961  <.0001
 Dierenrijk - ValleeDesSinges         -1.2575 0.200 Inf  -6.278  <.0001
 Frankfurt - Ouwehand                 -1.0165 0.165 Inf  -6.172  <.0001
 Frankfurt - Planckendael_Winter      -0.3861 0.158 Inf  -2.445  0.3757
 Frankfurt - Stuttgart1               -0.2595 0.206 Inf  -1.260  0.9839
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 Frankfurt - Stuttgart2                 -0.0842 0.208 Inf  -0.404  1.0000
 Frankfurt - Stuttgart3                  0.0386 0.252 Inf   0.153  1.0000
 Frankfurt - ValleeDesSinges             0.1897 0.152 Inf   1.249  0.9849
 Ouwehand - Planckendael_Winter          0.6304 0.164 Inf   3.843  0.0068
 Ouwehand - Stuttgart1                   0.7570 0.211 Inf   3.592  0.0171
 Ouwehand - Stuttgart2                   0.9323 0.213 Inf   4.375  0.0007
 Ouwehand - Stuttgart3                   1.0551 0.256 Inf   4.121  0.0022
 Ouwehand - ValleeDesSinges              1.2062 0.158 Inf   7.623  <.0001
 Planckendael_Winter - Stuttgart1        0.1265 0.206 Inf   0.616  1.0000
 Planckendael_Winter - Stuttgart2        0.3019 0.208 Inf   1.452  0.9530
 Planckendael_Winter - Stuttgart3        0.4247 0.252 Inf   1.687  0.8745
 Planckendael_Winter - ValleeDesSinges   0.5758 0.151 Inf   3.808  0.0078
 Stuttgart1 - Stuttgart2                 0.1753 0.246 Inf   0.711  0.9999
 Stuttgart1 - Stuttgart3                 0.2982 0.284 Inf   1.048  0.9965
 Stuttgart1 - ValleeDesSinges            0.4493 0.201 Inf   2.236  0.5230
 Stuttgart2 - Stuttgart3                 0.1228 0.286 Inf   0.429  1.0000
 Stuttgart2 - ValleeDesSinges            0.2739 0.203 Inf   1.347  0.9729
 Stuttgart3 - ValleeDesSinges            0.1511 0.248 Inf   0.609  1.0000
```

Annex 7: Table of dyadic significance between groups for YA

```
Pair of groups                         estimate    SE  df z.ratio p.value
 Antwerp - Apenheul                     0.47290 0.327 Inf   1.445  0.9545
 Antwerp - Beauval                     -0.10657 0.293 Inf  -0.364  1.0000
 Antwerp - Bussolengo                   0.44919 0.347 Inf   1.294  0.9801
 Antwerp - Dierenrijk                   0.47758 0.370 Inf   1.292  0.9803
 Antwerp - Frankfurt                    1.01130 0.311 Inf   3.256  0.0518
 Antwerp - Ouwehand                     0.12501 0.314 Inf   0.398  1.0000
 Antwerp - Planckendael_Winter          0.73757 0.307 Inf   2.406  0.4018
 Antwerp - Stuttgart1                   1.14417 0.417 Inf   2.746  0.2039
 Antwerp - Stuttgart2                   1.27469 0.441 Inf   2.889  0.1448
 Antwerp - Stuttgart3                   0.35246 0.481 Inf   0.733  0.9999
 Antwerp - ValleeDesSinges              0.55304 0.292 Inf   1.892  0.7648
 Apenheul - Beauval                    -0.57947 0.319 Inf  -1.815  0.8099
 Apenheul - Bussolengo                 -0.02371 0.370 Inf  -0.064  1.0000
 Apenheul - Dierenrijk                  0.00467 0.391 Inf   0.012  1.0000
 Apenheul - Frankfurt                   0.53839 0.335 Inf   1.605  0.9076
 Apenheul - Ouwehand                   -0.34789 0.338 Inf  -1.028  0.9971
 Apenheul - Planckendael_Winter         0.26467 0.332 Inf   0.798  0.9997
 Apenheul - Stuttgart1                  0.67126 0.435 Inf   1.541  0.9291
 Apenheul - Stuttgart2                  0.80179 0.459 Inf   1.747  0.8465
 Apenheul - Stuttgart3                 -0.12044 0.497 Inf  -0.242  1.0000
 Apenheul - ValleeDesSinges             0.08014 0.319 Inf   0.252  1.0000
 Beauval - Bussolengo                   0.55576 0.340 Inf   1.636  0.8958
 Beauval - Dierenrijk                   0.58414 0.363 Inf   1.611  0.9056
 Beauval - Frankfurt                    1.11787 0.302 Inf   3.700  0.0116
 Beauval - Ouwehand                     0.23158 0.305 Inf   0.758  0.9998
 Beauval - Planckendael_Winter          0.84414 0.298 Inf   2.833  0.1661
 Beauval - Stuttgart1                   1.25074 0.410 Inf   3.048  0.0952
 Beauval - Stuttgart2                   1.38126 0.435 Inf   3.173  0.0666
 Beauval - Stuttgart3                   0.45903 0.475 Inf   0.966  0.9983
 Beauval - ValleeDesSinges              0.65961 0.283 Inf   2.328  0.4563
 Bussolengo - Dierenrijk                0.02838 0.408 Inf   0.070  1.0000
 Bussolengo - Frankfurt                 0.56210 0.355 Inf   1.584  0.9152
 Bussolengo - Ouwehand                 -0.32418 0.358 Inf  -0.906  0.9991
 Bussolengo - Planckendael_Winter       0.28838 0.351 Inf   0.821  0.9996
 Bussolengo - Stuttgart1                0.69497 0.451 Inf   1.542  0.9289
 Bussolengo - Stuttgart2                0.82550 0.474 Inf   1.743  0.8480
 Bussolengo - Stuttgart3               -0.09673 0.510 Inf  -0.190  1.0000
 Bussolengo - ValleeDesSinges           0.10385 0.339 Inf   0.306  1.0000
 Dierenrijk - Frankfurt                 0.53372 0.377 Inf   1.416  0.9608
 Dierenrijk - Ouwehand                 -0.35257 0.380 Inf  -0.929  0.9988
 Dierenrijk - Planckendael_Winter       0.25999 0.374 Inf   0.696  0.9999
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 Dierenrijk - Stuttgart1                0.66659 0.468 Inf   1.424  0.9592
 Dierenrijk - Stuttgart2                0.79712 0.490 Inf   1.626  0.8999
 Dierenrijk - Stuttgart3               -0.12511 0.526 Inf  -0.238  1.0000
 Dierenrijk - ValleeDesSinges           0.07546 0.362 Inf   0.208  1.0000
 Frankfurt - Ouwehand                  -0.88629 0.322 Inf  -2.750  0.2017
 Frankfurt - Planckendael_Winter       -0.27373 0.315 Inf  -0.868  0.9994
 Frankfurt - Stuttgart1                 0.13287 0.423 Inf   0.314  1.0000
 Frankfurt - Stuttgart2                 0.26340 0.447 Inf   0.589  1.0000
 Frankfurt - Stuttgart3                -0.65883 0.486 Inf  -1.355  0.9716
 Frankfurt - ValleeDesSinges           -0.45826 0.301 Inf  -1.520  0.9354
 Ouwehand - Planckendael_Winter         0.61256 0.318 Inf   1.924  0.7443
 Ouwehand - Stuttgart1                  1.01916 0.425 Inf   2.395  0.4090
 Ouwehand - Stuttgart2                  1.14968 0.450 Inf   2.557  0.3043
 Ouwehand - Stuttgart3                  0.22745 0.488 Inf   0.466  1.0000
 Ouwehand - ValleeDesSinges             0.42803 0.305 Inf   1.405  0.9629
 Planckendael_Winter - Stuttgart1       0.40660 0.420 Inf   0.968  0.9983
 Planckendael_Winter - Stuttgart2       0.53712 0.445 Inf   1.208  0.9885
 Planckendael_Winter - Stuttgart3      -0.38511 0.484 Inf  -0.796  0.9997
 Planckendael_Winter - ValleeDesSinges -0.18453 0.297 Inf  -0.621  1.0000
 Stuttgart1 - Stuttgart2                0.13053 0.527 Inf   0.248  1.0000
 Stuttgart1 - Stuttgart3               -0.79170 0.560 Inf  -1.414  0.9611
 Stuttgart1 - ValleeDesSinges          -0.59113 0.410 Inf  -1.442  0.9552
 Stuttgart2 - Stuttgart3               -0.92223 0.578 Inf  -1.594  0.9117
 Stuttgart2 - ValleeDesSinges          -0.72165 0.435 Inf  -1.659  0.8865
 Stuttgart3 - ValleeDesSinges           0.20058 0.475 Inf   0.422  1.0000
```

Annex 8: Table of dyadic significance between groups for nose wiping

```
Pair of groups                         estimate    SE  df z.ratio p.value
 Antwerp - Apenheul                    -0.10435 0.215 Inf  -0.486  1.0000
 Antwerp - Beauval                      0.56861 0.198 Inf   2.879  0.1483
 Antwerp - Bussolengo                   1.10580 0.234 Inf   4.723  0.0001
 Antwerp - Dierenrijk                   0.90727 0.247 Inf   3.678  0.0126
 Antwerp - Frankfurt                    1.23569 0.204 Inf   6.064  <.0001
 Antwerp - Ouwehand                     0.69181 0.211 Inf   3.280  0.0482
 Antwerp - Planckendael_Winter          0.56218 0.201 Inf   2.800  0.1798
 Antwerp - Stuttgart1                   0.68794 0.262 Inf   2.629  0.2634
 Antwerp - Stuttgart2                   0.43511 0.262 Inf   1.658  0.8870
 Antwerp - Stuttgart3                   0.41693 0.315 Inf   1.322  0.9765
 Antwerp - ValleeDesSinges              0.65838 0.192 Inf   3.425  0.0302
 Apenheul - Beauval                     0.67296 0.210 Inf   3.211  0.0594
 Apenheul - Bussolengo                  1.21015 0.244 Inf   4.952  <.0001
 Apenheul - Dierenrijk                  1.01163 0.256 Inf   3.945  0.0046
 Apenheul - Frankfurt                   1.34004 0.215 Inf   6.219  <.0001
 Apenheul - Ouwehand                    0.79616 0.222 Inf   3.582  0.0177
 Apenheul - Planckendael_Winter         0.66653 0.213 Inf   3.134  0.0745
 Apenheul - Stuttgart1                  0.79229 0.271 Inf   2.924  0.1322
 Apenheul - Stuttgart2                  0.53946 0.272 Inf   1.986  0.7031
 Apenheul - Stuttgart3                  0.52128 0.323 Inf   1.613  0.9047
 Apenheul - ValleeDesSinges             0.76273 0.205 Inf   3.728  0.0105
 Beauval - Bussolengo                   0.53719 0.230 Inf   2.340  0.4477
 Beauval - Dierenrijk                   0.33866 0.242 Inf   1.397  0.9643
 Beauval - Frankfurt                    0.66708 0.199 Inf   3.360  0.0374
 Beauval - Ouwehand                     0.12320 0.206 Inf   0.598  1.0000
 Beauval - Planckendael_Winter         -0.00643 0.195 Inf  -0.033  1.0000
 Beauval - Stuttgart1                   0.11933 0.258 Inf   0.463  1.0000
 Beauval - Stuttgart2                  -0.13350 0.258 Inf  -0.517  1.0000
 Beauval - Stuttgart3                  -0.15168 0.312 Inf  -0.486  1.0000
 Beauval - ValleeDesSinges              0.08977 0.187 Inf   0.481  1.0000
 Bussolengo - Dierenrijk               -0.19852 0.273 Inf  -0.727  0.9999
 Bussolengo - Frankfurt                 0.12990 0.235 Inf   0.553  1.0000
 Bussolengo - Ouwehand                 -0.41399 0.241 Inf  -1.716  0.8612
 Bussolengo - Planckendael_Winter      -0.54361 0.232 Inf  -2.339  0.4484
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Bussolengo - Stuttgart1               -0.41785 0.287 Inf  -1.458  0.9517
Bussolengo - Stuttgart2               -0.67068 0.287 Inf  -2.334  0.4518
Bussolengo - Stuttgart3               -0.68886 0.336 Inf  -2.048  0.6604
Bussolengo - ValleeDesSinges          -0.44741 0.225 Inf  -1.988  0.7016
Dierenrijk - Frankfurt                 0.32842 0.247 Inf   1.327  0.9758
Dierenrijk - Ouwehand                 -0.21547 0.253 Inf  -0.850  0.9995
Dierenrijk - Planckendael_Winter      -0.34509 0.245 Inf  -1.408  0.9622
Dierenrijk - Stuttgart1               -0.21933 0.297 Inf  -0.738  0.9999
Dierenrijk - Stuttgart2               -0.47216 0.298 Inf  -1.586  0.9144
Dierenrijk - Stuttgart3               -0.49034 0.345 Inf  -1.420  0.9599
Dierenrijk - ValleeDesSinges          -0.24889 0.238 Inf  -1.046  0.9966
Frankfurt - Ouwehand                  -0.54389 0.212 Inf  -2.567  0.2987
Frankfurt - Planckendael_Winter       -0.67351 0.202 Inf  -3.337  0.0402
Frankfurt - Stuttgart1                -0.54775 0.263 Inf  -2.087  0.6325
Frankfurt - Stuttgart2                -0.80058 0.263 Inf  -3.042  0.0967
Frankfurt - Stuttgart3                -0.81876 0.316 Inf  -2.590  0.2849
Frankfurt - ValleeDesSinges           -0.57731 0.193 Inf  -2.987  0.1122
Ouwehand - Planckendael_Winter        -0.12962 0.209 Inf  -0.620  1.0000
Ouwehand - Stuttgart1                 -0.00386 0.268 Inf  -0.014  1.0000
Ouwehand - Stuttgart2                 -0.25669 0.269 Inf  -0.955  0.9985
Ouwehand - Stuttgart3                 -0.27487 0.321 Inf  -0.857  0.9995
Ouwehand - ValleeDesSinges            -0.03342 0.201 Inf  -0.166  1.0000
Planckendael_Winter - Stuttgart1       0.12576 0.260 Inf   0.483  1.0000
Planckendael_Winter - Stuttgart2      -0.12707 0.261 Inf  -0.487  1.0000
Planckendael_Winter - Stuttgart3      -0.14525 0.314 Inf  -0.462  1.0000
Planckendael_Winter - ValleeDesSinges  0.09620 0.190 Inf   0.506  1.0000
Stuttgart1 - Stuttgart2               -0.25283 0.310 Inf  -0.815  0.9997
Stuttgart1 - Stuttgart3               -0.27101 0.356 Inf  -0.761  0.9998
Stuttgart1 - ValleeDesSinges          -0.02956 0.254 Inf  -0.117  1.0000
Stuttgart2 - Stuttgart3               -0.01818 0.357 Inf  -0.051  1.0000
Stuttgart2 - ValleeDesSinges           0.22327 0.254 Inf   0.878  0.9993
Stuttgart3 - ValleeDesSinges           0.24145 0.309 Inf   0.782  0.9998
```