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Neighbors, Pros and Cons: Impact of Intergroup Interactions on the Welfare of Captive Chimpanzee Groups (*Pan troglodytes*)

Jose Gil-Dolz [1,*], Pablo R. Ayuso [1], David Riba [1,2] and Dietmar Crailsheim [1]

[1] Research Department, Fundació MONA, 17457 Girona, Spain; pablo.bio.uah@hotmail.com (P.R.A.); dribacano@gmail.com (D.R.); recerca@fundacionmona.org (D.C.)
[2] Facultad de Lletres, Universitat de Girona, Barri Vell Campus, 17004 Girona, Spain
* Correspondence: gildolzjose@gmail.com

Abstract: Housing different animal groups in close-by facilities is common in wildlife centers. However, the impact on animal welfare is insufficiently studied in the literature. In this study, we analyzed the behavior of two adjacently housed chimpanzee groups to investigate how intergroup interactions may affect their behavior and, thus, their welfare. We recorded occurrences of abnormal and self-directed behaviors, two well-known indicators of stress in chimpanzees. Furthermore, we explored the social responses to said intergroup interactions by recording all inter- and intragroup affiliative and agonistic behaviors. Finally, we measured the number of vigilance occurrences that individuals directed towards other chimpanzees as an indicator of interest. Generalized Linear Mixed Models (GLMMs) were used to assess whether and how social interactions between neighboring groups might influence their behaviors, taking gender, age, group, and intergroup participation into account. Our results suggest that intergroup interactions promoted the occurrence of affiliative behaviors between group members. However, intergroup interactions caused the chimpanzees to exhibit a higher number of abnormal and self-directed behaviors and increased vigilance towards their group members when agonistic intergroup interactions occurred. Thus, adjacent housing does impact the chimpanzees' behavior and welfare and should be continuously monitored and assessed to promote and maximize welfare.

Keywords: welfare; social interactions; intergroup; chimpanzees; primates; captive populations; well-being; sanctuary

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1. Introduction

Studies focusing on animal welfare in captivity [1], conducted at industrial production farms, zoological gardens, sanctuaries, and/or research centers [2–5], have helped create an ever-growing knowledge pool regarding the animals' needs and capacities. The obtained information is being used to improve animal care procedures and their living conditions and to raise awareness, thus leading to society's increasing concern regarding the quality of life of animals in captivity [6,7]. As a consequence, over the last few decades, more and more organizations housing wildlife in captivity conduct welfare assessments based on certain concepts, such as QoL (Quality of life) [8,9] or the Five Domains model, [10,11] and place increased emphasis on monitoring and improving the animals' welfare state. Taking into consideration that positive welfare requires negative factors to be minimized while promoting positive factors, housing organizations need to provide an adequate environment and opportunities to facilitate these states [12].

The enclosure complexity and design of captive environments often simulate or attempt to replicate aspects of the natural habitat [13–16]; dietary plans and feeding procedures are based on each species' nutritional needs, as well as the type of items they would find in the wild [17]. Enrichment programs are established to provide additional stimulation and to encourage species-specific behaviors [18–20]. Yet the most challenging aspect, in the case of social animals, including chimpanzees (*Pan troglodytes*), may be the provision of an adequate and functional social environment [21–23]. Considering that social partners potentially provide continuously changing stimulation and challenges, it can be understood as one of the most important and essential environmental factors to promote welfare in captively housed social animals [22,24]. Nevertheless, if not carefully evaluated and managed, said social environment may also produce important and/or lasting negative effects on the animal's behavior and welfare [25–27].

In the wild, chimpanzees may be found living in communities of up to 150 individuals, structured in hierarchical multimale and multifemale societies [28–30]. Individuals of one community are rarely seen altogether, as they typically separate into smaller subgroups (parties) based on fission–fusion dynamics, but they frequently meet up to shuffle, exchange party members, and separate again [30,31]. Several studies on a variety of species argue that fission–fusion dynamics arose to reduce intragroup competition for resources, such as food as well as access to sexually receptive females [32–36]. This social system requires chimpanzees to possess advanced social skills to navigate these flexible and complex social networks and to allow them to adapt to continuously changing group sizes and compositions [37–40]. However, captive chimpanzee groups tend to be much smaller [22,41], often lacking recommended age diversity and having unbalanced sex ratios [42] when compared to wild conspecifics. Furthermore, changes to the group formation, comparable to fission–fusion dynamics in the wild, tend to be much less frequent in captivity or mostly decided by care management staff, further reducing the amount of potential interaction partners, social stimulation, and opportunities.

Several studies in chimpanzees have demonstrated that unstimulating social environments are likely to produce a negative influence on the chimpanzees' overall behavior and welfare, while social environments offering more variety and opportunities may promote positive welfare [21,24,43,44]. For example, Webb et al. [21] reported that captive chimpanzee groups consisting of seven or more individuals and with a wide age range tend to exhibit higher levels of locomotion and/or higher levels of social interactions, depending on the sex ratio. Similarly, in the study conducted by Lehmann et al. [44], larger chimpanzee groups, i.e., chimpanzees with access to more potential interaction partners, were reported to spend more time on social grooming than individuals housed in smaller groups.

In addition to the limitations of reduced social opportunities experienced by captive chimpanzees at the intragroup level (between members of the same group), they rarely have the opportunity to interact with individuals outside of their own/natal group either. In the wild, we can find several types of interactions between chimpanzees from different communities, ranging from female immigration patterns [45] to long-distance communications [46–48] and direct confrontations between chimpanzees patrolling their territories [49–51]. For example, long-distance communication is common among chimpanzee groups in the wild, both between troupes who are part of the same community as well as between different communities [46–48]. Direct encounters between different groups have also been documented, often marked by intense dominance or bluff-displaying behavior as well as physical aggression and wounding, being part of the species' typical patrolling and territorial defense behavior, carried out primarily by adult males of each group [48,52]. These direct intergroup conflicts can become very violent, producing numerous injuries, including the loss of body parts or even death [49,53]. Nevertheless, it is worth mentioning that on rare occasions there have been reports of affiliative interactions between chimpanzees belonging to different groups, as well [51].

Although social complexity is important for chimpanzee welfare, centers are often unable to provide these conditions for their animals due to a variety of resource constraints [22]. Such constraints may be due to physical limitations of enclosure size and/or design, specific care management needs, and/or incompatibilities between individuals, i.e., risk of lethal or repetitive injury between group members. Furthermore, centers that do not form part of any breeding projects and/or use birth control will likely encounter a lack of age diversity over time and find that captive populations grow older on average, with a strongly skewed age distribution [54]. Considering the available resources, it can be a challenge for housing organizations to meet the social needs of these animals by providing them with a stimulating and welfare-enhancing social environment. Nevertheless, for organizations facing limitations restricting their capacity to establish and maintain larger and more diverse social groups, one possible method to increase social complexity and provide more potential social partners as well as opportunities could be to house separate social groups in adjacent or close-by facilities/enclosures that allow auditory and/or visual contact at the very least. In this way, chimpanzees could interact partially, that is, via non-physical interactions with individuals from another group, without the risk of such interactions resulting in a violent physical confrontation, potentially leading to health and/or care management issues. While there are organizations that house their chimpanzees in this manner because it facilitates effective care, others recognize the potential welfare benefits of housing different groups of chimpanzees in contiguous habitats, as well.

However, to our knowledge, reports and research regarding this topic in great apes are scarce. For example, Grand and colleagues [55] studied the impact of how the proximity between enclosures affected the behavior of a bachelor and a family group of gorillas (*Gorilla gorilla*). Other studies on chimpanzees demonstrated how auditory information, such as, for example, hearing other chimpanzees socially interacting from physically and visually separated groups, produced a contagious effect on the social dynamics of adjacently housed individuals [56]. Gil-Dolz and colleagues [57] reported that interactions between two physically separated groups of chimpanzees housed in adjoining habitats occurred frequently enough that they were considered to be in the animals' social networks, thus producing an augmentation of the complexity of their social networks. However, to our knowledge, so far no information has been published on how such interactions between groups may impact the chimpanzees' behavior and, in continuation, their well-being in captivity.

Thus, the main objective of the present study is to follow up on the previously mentioned study conducted by Gill-Dolz and colleagues [57] to assess how interactions between two captive groups of chimpanzees housed in adjoining habitats influence the individuals' behavior and social dynamics within each group. Specifically, we are expecting to find that (1) agonistic intergroup interactions will produce an increase in self-directed and abnormal behaviors; (2) agonistic intergroup interactions will produce an increase in agonistic inter- and intragroup interactions; (3) agonistic intergroup interactions will increase the frequency of affiliative interactions between members of the same group; and (4) affiliative intergroup interactions will have a neutral impact on or produce an increase in the affiliative interactions between group members.

2. Materials and Methods

2.1. Subjects and Study Site

The study population consisted of two adjointly housed social groups of former pet and entertainment chimpanzees ($N = 10$; Table 1) housed at the primate rescue and rehabilitation center Fundació MONA, located in the north of Spain, Cataluña. The center is a member of the European Alliance of Rescue Centers and Sanctuaries (EARS), and it has been providing life-long care to rescued primates since 2001. At the time of data collection, all chimpanzees were adults (4 females and 6 males), ranging between 20 to 41 years of age (mean age: 29.60, SD: ±7.69). Both groups of chimpanzees, "Mutamba" and "Bilinga", consisted of 5 chimpanzees, with 3 males and 2 females each (mean age Mutamba: 26.60, SD: ±7.36; mean age Bilinga: 32.6, SD: ±7.50). Depending on their age, animals were labeled as adults or seniors, with seniors being 35 years of age or older (only three males were labeled as seniors in our sample). Following regulations established for rescue centers and sanctuaries, all females in the study sample were given oral contraceptive treatment. All individuals had been living at the center within a stable social group for at least six years and were accustomed to being housed in proximity to other chimpanzee groups. Indoor areas of the adjacently housed groups were located within the same building, allowing them to hear but not see each other. To learn more about the behavioral profiles of the animals, their housing conditions, and group alterations during the previous years, see [58].

Table 1. Characteristics of the study population.

Name	ID	Sex	Year of Birth	Group
África	AFR	F	2000	Mutamba
Bongo	BON	M	1999	Mutamba
Juanito	JUA	M	2003	Mutamba
Marco	MAR	M	1984	Mutamba
Waty	WAT	F	1996	Mutamba
Tom	TOM	M	1985	Bilinga
Cheeta	CHE	F	1990	Bilinga
Coco	COC	F	1994	Bilinga
Nico	NIC	M	2001	Bilinga
Víctor	VIC	M	1982	Bilinga

Abbreviations: F = female; M = male.

Observations were conducted between 10:00 and 18:00 while both chimpanzee groups had access to their respective outdoor enclosures (Mutamba: 2420 m^2; Bilinga: 3220 m^2). The chimpanzees were housed in two adjacent outdoor enclosures divided by a steel mesh and an electrified fence (Figure 1). Thus, animals belonging to different groups could get as close as 60 cm to each other, see and hear each other, and interact socially, but physical contact was completely prevented by the fencing system installed between the outdoor enclosures. All chimpanzees were already accustomed to the security measures separating the two groups, and at no time did they attempt to physically touch a chimpanzee from the neighboring group. Said outdoor habitats consisted of naturalistic terrain with Mediterranean vegetation, additionally equipped with several artificial climbing structures, such as towers, wooden platforms, bridges, ropes, and daily changing enrichment devices. During night time or when the climatic weather conditions were not appropriate, all chimpanzees were restricted to their indoor facilities (140 m^2). For more detailed information regarding their indoor and outdoor facilities, care management, and feeding routines, see [59,60].

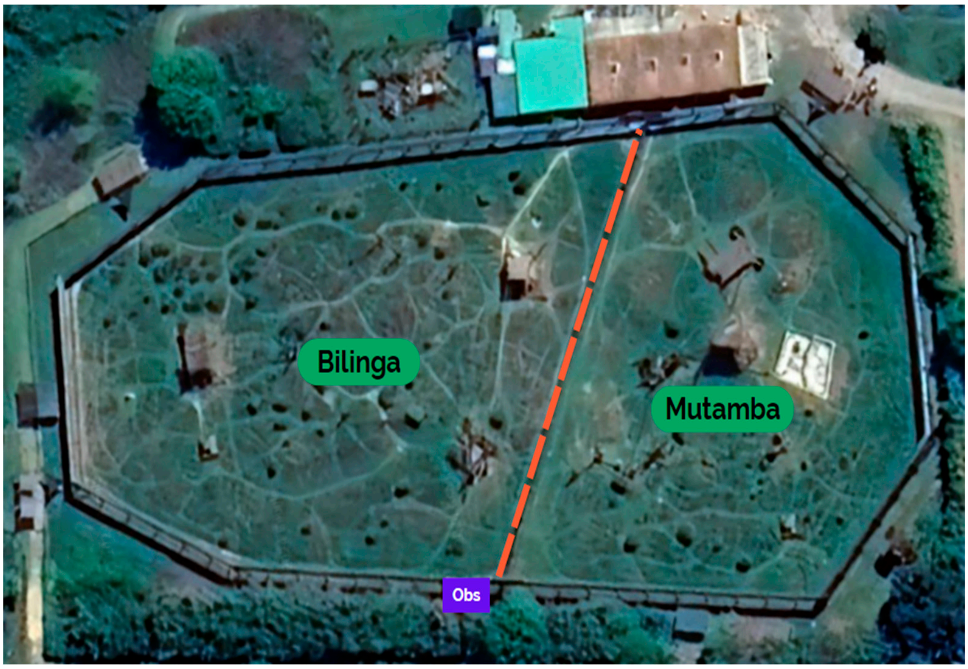

Figure 1. The satellite image depicts the two outdoor chimpanzee habitats (marked with their group names), separated by an electrified fence (marked in red), and the observation tower (marked in blue "Obs") from which all observations were conducted [61].

2.2. Data Sampling

All observations were conducted from a single observation tower (Figure 1), located at the edge of the chimpanzee outdoor enclosures near the end of the separating fence. This location was chosen to maximize visibility of areas where individuals from different groups could see and socially interact across the fence.

A total of three observers recorded the chimpanzees' behavior for 65 days, randomly distributed over five months between October 2023 and February 2024, resulting in a total of 147.33 h of multifocal group observations (Table 2). During the absence of social intergroup interactions, observers recorded baseline observations. Apart from baseline observations, observation sessions were initiated by one or several chimpanzees exhibiting social interaction towards members of the neighboring group (intergroup affiliative or agonistic behaviors), i.e., the observer started observing the behavioral response of the group receiving the initial intergroup interaction. All observation sessions, both triggered by intergroup interactions or in its absence, lasted for 20 min. Following this methodology, observers recorded 125 h (Mutamba 67 h; Bilinga 58 h) in the absence of social interactions between groups (baseline) and a total of 22.33 h of intergroup interaction (Mutamba 4.7 h; Bilinga 17.7 h). Sessions initiated by intergroup interactions were labeled according to the nature of the initial trigger interaction as "affiliative" or "agonistic".

Table 2. Observation hours and number of sessions collected in each condition and group.

	Baseline		**Affiliative Trigger**		**Agonistic Trigger**	
	Sessions	**Hours of Observation**	**Sessions**	**Hours of Observation**	**Sessions**	**Hours of Observation**
Total	375	125	24	8	43	14.33

Observers were trained over several weeks in behavioral data collection at Fundació MONA and only started collecting data for this specific project after successfully passing a three-tier interobserver reliability test. The first step included data collection over two weeks; these data were checked and eventually deleted. In the second step, observers had to pass a methodology test, and, in the third step, they had to pass a video test by identifying animals and behaviors with an agreement of ≥85% with the primary researcher of this publication.

Behavioral data were collected on tablet devices equipped with the digital data collection software Zoomonitor [62], using multifocal (all members of one social group) All Occurrence [63] methodology. Therefore, observers recorded all occurrences of abnormal, self-directed, vigilance, and social behaviors, such as agonistic and affiliative behaviors (Table S1). A behavior was scored again if the observed chimpanzee stopped performing said behavior and exhibited another unrelated behavior for more than 5 s.

2.3. Data Analysis

In order to investigate whether intergroup interactions affected chimpanzee welfare, eight Generalized Linear Mixed Models (GLMMs) [64] were run using the package *glmmTMB* [65] in the R programming environment (version 4.3.2) [66]. For this purpose, the occurrences of abnormal and self-directed behaviors (Models 1 and 2) performed by chimpanzees in the different session-triggering conditions were counted (Table S2). In this regard, we also recorded the occurrences of social, affiliative, and agonistic behaviors performed by chimpanzees to members of their own group (Models 3 and 5) and to individuals from the neighboring group (Models 4 and 6) (Table S2). Finally, we explored how the three conditions (baseline, affiliative-triggered, and agonistic-triggered) affected the occurrences of vigilance performed by chimpanzees to members of their own group (Model 7) and to chimpanzees in the adjacent enclosure (Model 8) (Table S2). All models were constructed using the session-triggering conditions as predictor variables (baseline, affiliative, or agonistic) and age, sex, group, and intergroup participation as control variables. Age was transformed into a categorical variable with two levels, adult or senior. If chimpanzees were 35 years of age or older at the start of the study, they were considered seniors. The typical frequency of an individual's participation in intergroup interactions was also included as a control variable. Through an exploratory analysis of the data, this variable was also categorized into two levels: "occasional" when eight or less occurrences of participation with individuals of the other group were recorded, and "frequent" when the frequency of participation was greater than eight occurrences. The levels were cut empirically with visual inspection of the data distribution using histograms. Because the affiliative interactions between groups were only performed by males and all of them were categorized as frequent participants in intergroup interactions, we had to eliminate the sex and participation variables from Model 4 to avoid errors in the statistical analyses. Finally, the individual's ID was added to all models as a random factor.

Models containing all predictors and control variables (full) were compared with models containing only the random factors and controls (null) by means of an ANOVA likelihood test [67]. If the full model differed from the null model at a significance level of 0.05, the *drop1* function was used to obtain the *p*-value for each predictor variable [68]. Finally, to rule out collinearity between predictor variables, variance inflation factors were calculated [69], which were very good in all models (maximum VIF between models = 2.46). Finally, to establish post hoc comparisons between the three types of experimental conditions, we used Tukey's tests in the emmeans package [70].

3. Results

We ran a total of eight GLMMs to investigate the potential impact of intergroup interactions on the behavior of the neighboring chimpanzees, while considering the condition of the triggering intergroup behavior (affiliative vs. agonistic vs. base) and the receiving chimpanzee´s sex (male vs. female), age (adult vs. senior), group (Bilinga vs. Mutamba), as well as intergroup participation (occasional vs. frequent). Out of the eight models, four models were significantly improved when comparing the full models with their corresponding null models (Table S2). The significant models were Model 1 (abnormal behaviors), Model 2 (self-directed behaviors), Model 3 (affiliative intragroup behaviors), and Model 7 (intragroup vigilance), while Model 4 (affiliative intergroup behaviors), Model 5 (agonistic intragroup behaviors), Model 6 (agonistic intergroup behaviors), and Model 8 (intergroup vigilance) were not improved by any of the fixed factors.

In Model 1 (abnormal behaviors), the full model differed significantly from the null model (GLMM: $\chi^2 = 23.629$, gl = 2, $p < 0.001$), with condition being the only significant factor ($p < 0.001$). Baseline condition had a negative association with the number of occurrences of abnormal behavior (Table S2). Post hoc analyses revealed that chimpanzees performed a greater number of abnormal behaviors after the occurrence of affiliative (affiliative–baseline: z = 4.318; $p < 0.001$) or agonistic (agonistic–baseline: z = 3.584; $p < 0.001$) intergroup interactions in comparison to baseline sessions (Table S3). Confidence interval plots regarding the significant factor are shown in Figure 2.

In Model 2 (self-directed behaviors), the full model also differed significantly from the null model (GLMM: $\chi^2 = 10.934$, gl = 2, $p < 0.01$), with condition ($p < 0.01$) and age ($p < 0.05$) significantly impacting the chimpanzees' self-directed behaviors (Table S2). Regarding the condition, we found that self-directed behaviors were negatively associated with baseline sessions, and post hoc analyses revealed that chimpanzees performed a greater number of more self-directed behaviors after the occurrence of affiliative (affiliative–baseline: z = 2.727; $p < 0.05$) and agonistic (agonistic–baseline: z = 2.319; $p = 0.05$) intergroup interactions, in comparison to baseline sessions (Table S3). Confidence interval plots regarding the significant factors are shown in Figure 3.

In Model 3 (intragroup affiliative behaviors), the full model differed significantly from the null model (GLMM: $\chi^2 = 25.024$, gl = 2, $p < 0.001$). As in the previous two models, condition ($p < 0.001$) was a significant factor, providing insights regarding the observed differences in the number of occurrences of intragroup affiliative behaviors (Table S2). Specifically, we found that in the absence of intergroup interactions (baseline), chimpanzees performed fewer affiliative interactions with group members. With respect to age, we found that individuals categorized as "senior" exhibited more abnormal behaviors. As in Model 1, the baseline condition had a negative relationship with the dependent variable (self-directed). Post hoc analyses supported these results, as chimpanzees performed more affiliative intragroup behaviors when affiliative (affiliative–baseline: z = 4.606; $p < 0.001$) or agonistic (agonistic–baseline: z = 3.081; $p < 0.01$) interactions occurred between the two groups (Table S3).

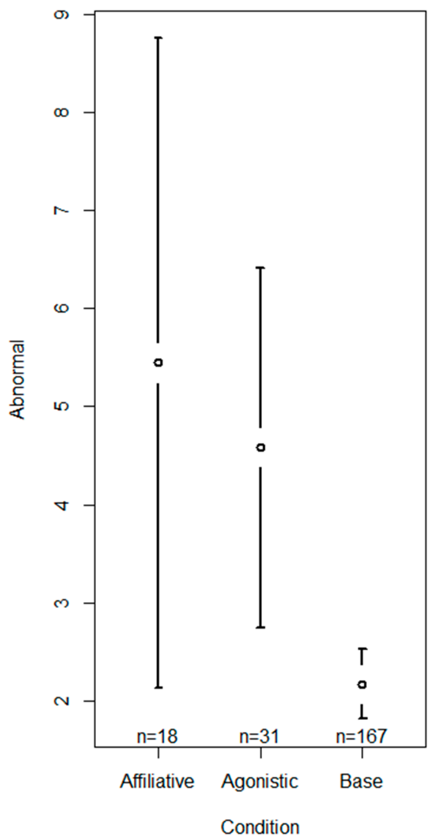

Figure 2. Confidence interval plots of abnormal behaviors and the significant variable-triggering condition. The *Y*-axis corresponds to the relative frequency of the observed abnormal behaviors (occurrences per 20 min observation session). The "n" refers to the number of sessions triggered by the different conditions.

Sex ($p < 0.05$), group ($p < 0.001$), and participation ($p < 0.01$) were also significant variables in explaining differences in the number of occurrences of affiliative behaviors directed at chimpanzees in the other group (Figure 4, Table S2). Males directed fewer affiliative behaviors towards members of the other group than females. In addition, those individuals who were more likely to engage in intergroup interactions (i.e., frequent participants) engaged in fewer affiliative intergroup interactions. Regarding the fixed factor group, individuals from the Mutamba group generally engaged in more affiliative behaviors towards the other group than members from the Bilinga group. Confidence interval plots regarding the significant factors are shown in Figure 4.

In Model 7 (intragroup vigilance), the full model differed significantly from the null model (GLMM: $\chi^2 = 6.068$, gl = 2, $p = 0.048$), with condition ($p < 0.05$) being the only significant factor (Table S2). Post hoc analyses showed that there were significant differences between intragroup vigilance behaviors performed during agonistic interaction sessions and baseline sessions (agonistic–baseline. z = 2.413; $p < 0.05$) (Table S3). Confidence interval plots regarding the significant factors are shown in Figure 5.

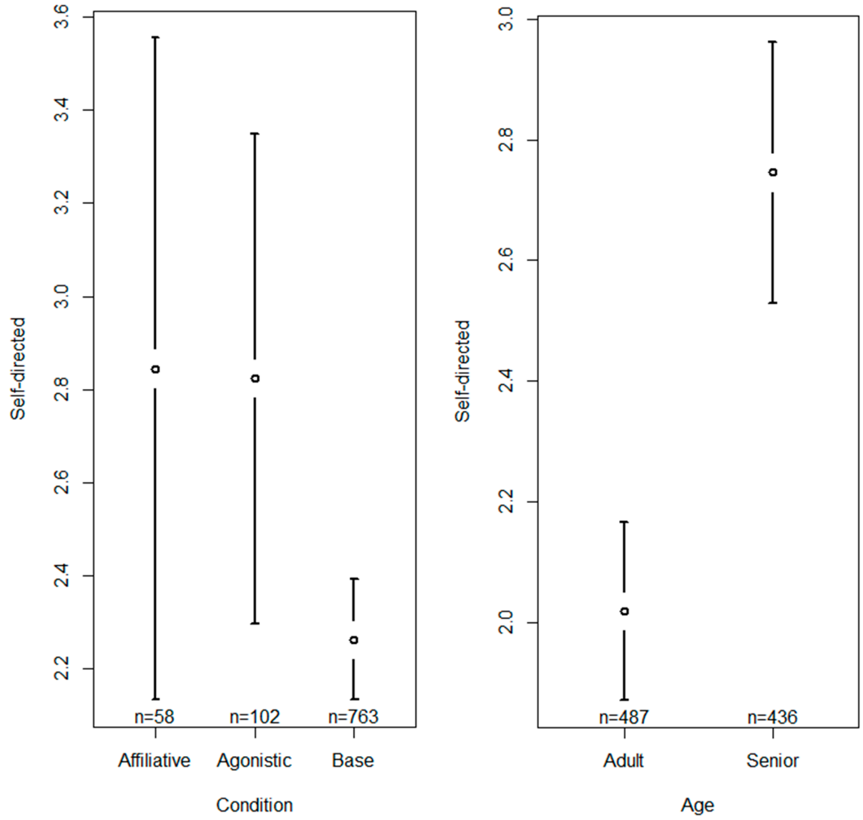

Figure 3. Confidence interval plots of self-directed behaviors and the significant variables triggering condition and age. The *Y*-axis corresponds to the relative frequency of the observed self-directed behaviors (number of occurrences per 20 min observation session). The "n" refers to the number of sessions triggered by the different conditions.

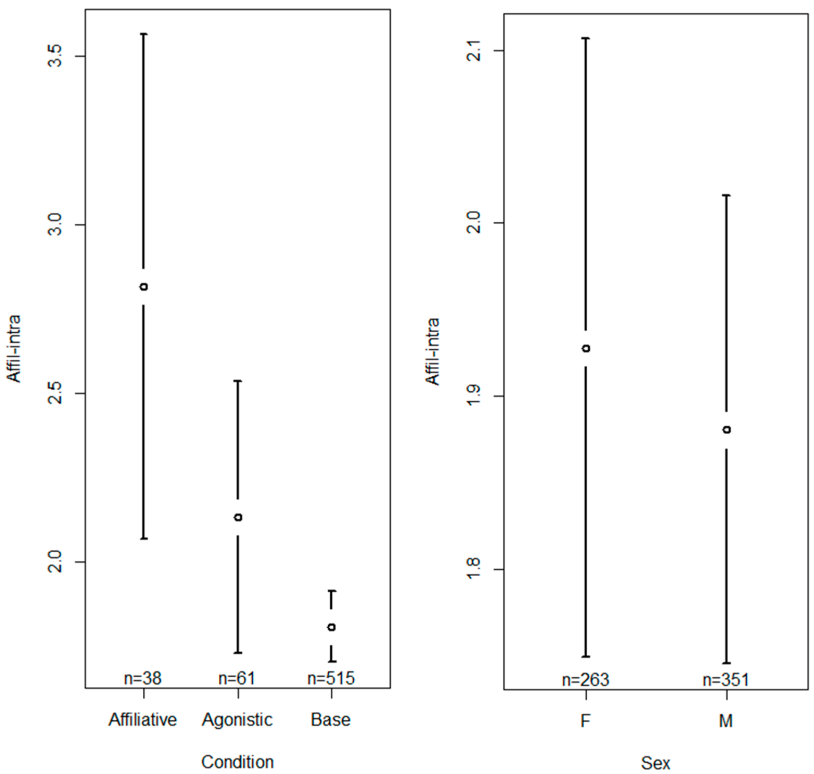

Figure 4. *Cont*.

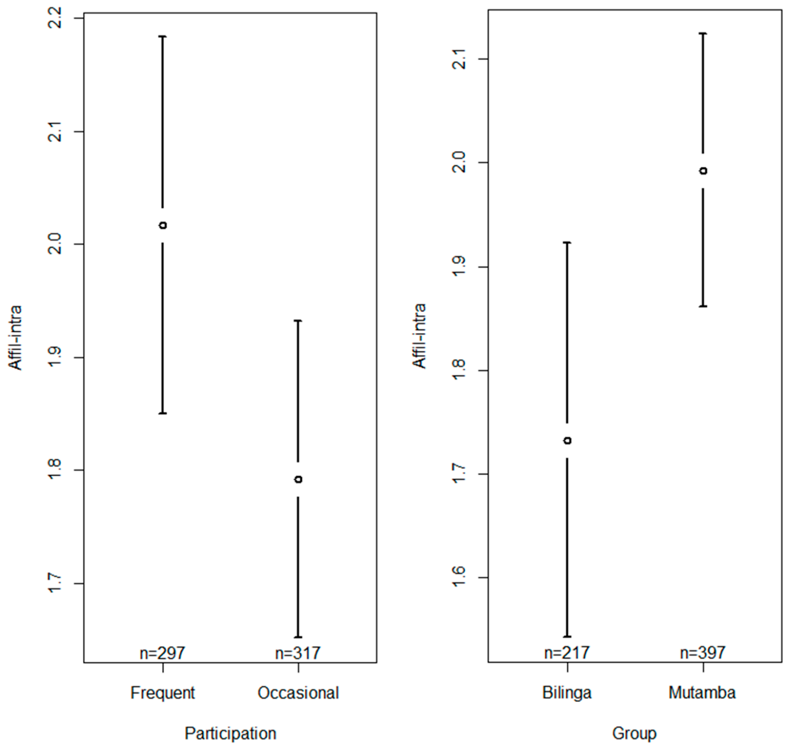

Figure 4. Confidence interval plots of intragroup affiliative behaviors and the significant variables condition, sex, participation, and group. The *Y*-axis corresponds to the relative frequency of the observed affiliative intragroup interactions (number of occurrences per 20 min observation session). The "n" refers to the number of sessions triggered by the different conditions.

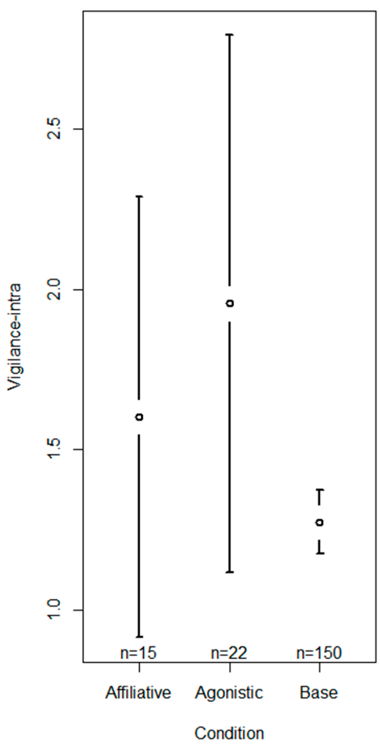

Figure 5. Confidence interval plots of intragroup vigilance behavior and the significant variable triggering condition. The *Y*-axis corresponds to the relative frequency of the observed vigilance behavior directed to members of their own group (number of occurrences per 20 min observation session). The "n" refers to the number of sessions triggered by the different conditions.

4. Discussion

As expected, our results indicate that intergroup interactions between the two observed groups of chimpanzees produce an impact on their social and individual behavior. We found that during and after these intergroup interactions, affiliative behaviors among chimpanzees from the same group (Model 3) would increase significantly (Figure 4). Furthermore, this augmentation in affiliative intragroup interactions occurred independently of the type of social intergroup interaction; that is, chimpanzees of the same group would exhibit affiliative interactions more frequently during both sessions that were initially triggered by affiliative as well as agonistic intergroup interactions. An increase in affiliative intragroup interactions during and/or following affiliative intergroup interactions could be explained by social contagion, i.e., chimpanzees would be more likely to engage in affiliative behaviors with group members when seeing other chimpanzees in their surroundings engage in affiliative interactions (for example, group members interacting with neighboring chimpanzees in an affiliative manner). During the last few decades, several studies have been published focusing on behavioral contagion in non-human primates, with some concentrating on the contagion of agonistic behaviors [71–73] while others relate to the contagion of affiliative behaviors [74,75]. For example, Ostner and colleagues [75] concluded that female rhesus macaque (*Macaca mulatta*) are more likely to perform grooming behaviors due to visual contagion (that is, witnessing other group members performing these affiliative behaviors beforehand). However, to date, few studies have been published exploring the contagion of affiliative behaviors in chimpanzees [56,76]. In a study conducted by Videan and colleagues [56], they were able to demonstrate that hearing grooming vocalizations encouraged chimpanzees from other groups (who could hear but not see the grooming activity) to engage in social grooming with their group members. More recently, observations conducted in a master's thesis [76] reported clear evidence of behavioral contagion, suggesting that chimpanzees were more likely to participate in grooming interactions and social play activities after observing others exhibiting said behaviors. Considering these findings as well as behavioral contagion reported in other species, we believe the increase in frequency of affiliative behaviors recorded here during observation sessions triggered by affiliative intergroup interactions is likely also related to social contagion dynamics.

On the other hand, our results also indicate that affiliative intragroup interactions did increase significantly in sessions triggered by agonistic intergroup interactions. One possible explanation might be that agonistic behaviors received from one or several individuals from a neighboring group could be perceived as an external outgroup threat, which has been observed and frequently described in wild populations. Such a perception of a common external threat could lead to an increase in affiliative intragroup interactions aiming to reinforce group cohesion [30,77]. While intragroup support is one possibility, especially when occurring during an agonistic confrontation between groups, another possible explanation might be group members offering consolation and comfort via affiliative interactions, such as grooming, after an intergroup confrontation [78,79]. Several studies in chimpanzees [80–82] and other non-human primates [83–85] describe the patterns and importance of reconciliation and consolation dynamics after agonistic intragroup events, i.e., conflict participants and/or those not directly involved engage in affiliative behaviors to make peace, treat injuries, and/or comfort each other [79,86,87]. Furthermore, chimpanzees that were labeled frequent intergroup participants (in both agonistic and affiliative interactions) were generally also socially more active within their social group, exhibiting frequent grooming and other intragroup affiliative behaviors.

Thus, chimpanzees observed to interact more frequently with individuals from the other group were also more likely to exhibit affiliative behaviors in situations that could be explained by social contagion, intragroup cohesion, and/or consolation. Contrary to many studies on wild populations reporting that affiliative interactions (especially grooming) tend to be much more frequent between male chimpanzees [83], our data show males performing fewer affiliative behaviors than females. Although our data show that only males participated in intergroup affiliative interactions, females in our population exhibited more affiliative behaviors with individuals in their own group. These findings on the social activity of female chimpanzees are consistent with several studies conducted in captivity, which suggest that females tend to be more socially active in captivity due to the absence of certain factors, such as resource competition and dispersal patterns [88]. Besides differences based on the individual's sex, we also found a clear difference in affiliative interaction frequency between both groups, with the Mutamba group exhibiting affiliative intragroup interactions much more frequently, regardless of the context. Considering that the groups' sex ratio, group size, and external factors, such as enclosure design and care management, are identical, these differences could be due to their age distribution (Mutamba only contains one senior chimpanzee), differences in their upbring and adverse early life experiences [89], and/or differences in personality [90]. This tendency is not limited to the affiliative behaviors but can also be observed in the frequency of agonistic behaviors exhibited (Figure S2).

Regardless of the initial intergroup interaction (either affiliative or agonistic) that initiated the observation session, no difference was observed in the frequency of intergroup interactions, nor in their affiliative or agonistic responses. We specifically expected agonistic intergroup interactions to produce an increase in both agonistic inter- as well as intragroup interactions. The increase in agonistic intergroup interactions was suspected to occur as a direct response to the initial agonistic trigger interaction between groups, while an increase in agonistic intragroup interactions was expected due to potential unresolved tensions and/or behavioral contagion. Nevertheless, our results suggest that agonistic interactions between individuals from different groups do not necessarily increase the exhibition of agonistic behaviors in any way. Thus, while affiliative intergroup interactions produce more frequent affiliative intragroup interactions, agonistic behaviors do not follow the same pattern. As explained previously, one very common care management reason to maintain several smaller chimpanzee groups rather than bigger groups is the occurrence of extreme or recurring aggressions leading to serious or fatal injuries. Offering (physically limited) access to adjacent housed groups would still allow for the possibility to express agonistic and/or dominance-related display behaviors, i.e., allow chimpanzees to express these behaviors and potentially get rid of pent-up tension, yet without the risk of injuries due to the separating fencing system. We therefore conclude that intergroup social interactions in our study population can be understood to contribute positively to the welfare of these chimpanzees, as they increase social complexity by providing more potential low-risk relationship partners and lead to a general increase in affiliative responses but not agonistic intragroup responses. One possible explanation for the chimpanzees' lack of response to agonistic interactions is that chimpanzees in our sample were already accustomed to the displays of individuals from the other group. Thus, unless the intergroup conflict is very serious or something could be gained by responding in kind, such as demonstrating their physical capacities to group members without directing the behavior at the group members themselves, chimpanzees would opt to ignore the provocations of their neighbors.

Although we did not observe a direct negative impact of agonistic interactions on their social behaviors, in accordance with our predictions, agonistic interactions between groups did cause an increase in abnormal and self-directed behaviors (Figure 3). It is well-documented that chimpanzees increase the frequency and/or intensity of self-directed behaviors, such as yawning, scratching, as well as abnormal or stereotypical behaviors, when facing stressful situations [91–95]. Furthermore, several studies have reported a direct relationship between such stress indicators and the initiation of conflicts in chimpanzee groups [73,96]. Baker and Aureli [73] even demonstrated that agonistic events produced in neighboring chimpanzee groups can promote the occurrence of self-directed behaviors in chimpanzees that were not involved in these conflicts. Although we did not find any literature that clearly states agonistic events lead to more abnormal behaviors in chimpanzees, we still expected chimpanzees to increase the exhibition of abnormal behaviors due to the potential increase in stress from being involved in, targeted by, or in proximity to a conflict.

Considering that the chimpanzees in this population all have a history of adverse early living conditions, experiencing traumatic events, and suffering prolonged exploitation in the entertainment industry and/or as pets, they are likely to engage more frequently in abnormal behaviors during stressful situations [97].

Yet, self-directed and abnormal behaviors did not only increase during sessions triggered by agonistic intergroup interactions but were equally likely to occur more frequently during sessions triggered by affiliative intergroup interactions. A possible reason for the observed increase in stress-related behaviors could also be due to the chimpanzees experiencing frustration by not being able to physically interact with or follow chimpanzees from the neighboring group. Such a frustration effect can also be observed in other mammals in captivity, such as minks or pigs, where abnormal behaviors have been suggested to be motivated by frustration due to the animal's inability to physically interact with conspecifics due to the existence of physical barriers [98,99]. We also found that older chimpanzees (seniors) tended to perform more self-directed behaviors than younger chimpanzees (Figure 3, Table S2), which is in accordance with findings in other studies that found higher frequencies of self-directed behaviors in older chimpanzees (Figure 3, Table S2) [54,100,101].

The last two models (Models 7 and 8) focusing on vigilance behaviors suggest that chimpanzees would not alter their vigilance behavior towards the neighboring group much, regardless of the social intergroup context. Considering that vigilance can be understood as increased interest, caution, and/or attentiveness, they did not seem to feel the need to pay extra attention to the other group even after social intergroup interactions occurred. This might indicate a certain awareness of safety in terms of physical danger from members of the neighboring group. On the other hand, vigilance behaviors directed at members of their own group did increase during sessions that were triggered by agonistic intergroup interactions. This increase in vigilance behavior could be due to potentially increased tensions observed in members of one's own group triggered by an intergroup conflict that could, in continuation, lead to an intragroup agonistic event, resulting in a potential injury risk between members of the same group [102].

5. Conclusions

As expected, intergroup interactions had an impact on chimpanzees' behavior and thus, potentially, their overall welfare. In agreement with our predictions, intergroup affiliative interactions seemed to have a positive impact on the chimpanzees' social activity and provided additional social stimulation and complexity, as interactions between chimpanzees from different groups produced an increase in affiliative relationships within each group. Contrary to our predictions, yet evaluated as desired and positive in terms of welfare, agonistic behaviors directed at members from the neighboring group did not promote agonistic interactions at the intra- or intergroup level. Finally, in agreement with our first prediction, agonistic interactions led to an increase in abnormal and self-directed behaviors in chimpanzees. However, we did not expect affiliative interactions between members of both groups to produce the same result. In addition, chimpanzees were more attentive to their own group's activity when intergroup agonistic interactions occurred, which may reflect increased tension over whether conflict would be transferred within the group.

As already hypothesized in our previous article [57], we now provide more findings supporting the original argument that the adjacent housing of different chimpanzee groups has the potential to provide additional social relationship opportunities, i.e., increased social complexity and stimulation passively due to the proximity and visual and auditory contact as well as directly through direct intergroup interactions. However, we strongly desire to emphasize that while this could be understood as a purely welfare-promoting factor, an increase in social stimulation and complexity and, to a certain degree, forced proximity may potentially also produce undesired impacts, such as augmented stress levels and increases in inter- and/or intra-conflicts, which need to be continuously evaluated and monitored. We are aware that the sample size of this study is limited to only two groups of chimpanzees. We are currently reaching out to and working on replicating this project with other chimpanzee housing organizations to increase both the sample size and the variety and to collect some more details of interest regarding the individuals' biographic information. Likewise, we encourage and hope to motivate others to replicate this study and/or work on similar topics in order to help increase our ability to provide these animals with a suitable social environment in captivity.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/ecologies5020018/s1, Table S1: Ethogram used for multifocal All Occurrence data collection; Table S2: Results of the statistical models. For each model and predictor, estimators, standard errors (SEs), likelihood ratio tests (LRTs), degrees of freedom (gl), and *p*-values (p) are shown. Models 4–6 and 8 are not included in this table because no significant differences were found between the full model and the null model; Table S3: Results of the post hoc analysis of the statistical models. For each model and contrast, estimators, standard errors (SEs), z-scores (z), and *p*-values (p) are shown. Models 4–6 and 8 are not included in this table because no significant differences were found between the full model and the null model; Figure S1: Rate of affiliative behavior according to intergroup participation profiles: frequent or occasional; Figure S2: Graph showing the rates of affiliative, agonistic, and vigilance behaviors as a function of group (Mutamba or Bilinga) and type of interaction (intragroup or intergroup).

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References

1. Fernandez, E.J.; Martin, A.L. Animal Training, Environmental Enrichment, and Animal Welfare: A History of Behavior Analysis in Zoos. *J. Zool. Bot. Gard* **2021**, *2*, 531–543. [CrossRef]
2. Bayne, K.; Bayvel, A.C.D.; Williams, V. Laboratory Animal Welfare. In *American College of Laboratory Animal Medicine*; Bayne, K., Turner, P.V., Eds.; Academic Press: Boston, MA, USA, 2013; pp. 55–76. ISBN 978-0-12-385103-1.
3. Velarde, A.; Fàbrega, E.; Blanco-Penedo, I.; Dalmau, A. Animal Welfare towards Sustainability in Pork Meat Production. *Meat Sci.* **2015**, *109*, 13–17. [CrossRef]
4. Davey, G. Visitors' Effects on the Welfare of Animals in the Zoo: A Review. *J. Appl. Anim. Welf. Sci.* **2007**, *10*, 169–183. [CrossRef]
5. Padrell, M.; Amici, F.; Córdoba, M.P.; Giberga, A.; Broekman, A.; Almagro, S.; Llorente, M. Artificial Termite-Fishing Tasks as Enrichment for Sanctuary-Housed Chimpanzees: Behavioral Effects and Impact on Welfare. *Animals* **2021**, *11*, 2941. [CrossRef] [PubMed]
6. Broom, D.M. A History of Animal Welfare Science. *Acta Biotheor.* **2011**, *59*, 121–137. [CrossRef]
7. Koknaroglu, H.; Akunal, T. Animal Welfare: An Animal Science Approach. *Meat Sci.* **2013**, *95*, 821–827. [CrossRef] [PubMed]
8. Simpson, L.; Grove, J.; Bronson, E.; Herrelko, E.S. Quality of Life Assessment: The Value of Longitudinal Data in Making the End-of-Life Care Decision for a Macaque (*Macaca silenus/Macaca nemestrina*). *J. Appl. Anim. Welf. Sci.* **2024**, *27*, 316–329. [CrossRef]

9. Campbell-Ward, M. Quality-of-Life Assessments in Zoo Animals: Not Just for the Aged and Charismatic. *Animals* **2023**, *13*, 3394. [CrossRef] [PubMed]
10. Mellor, D.J.; Reid, C.S.W. Concepts of Animal Well-Being and Predicting the Impact of Procedures on Experimental Animals. In *Improving the Well-Being of Animals in the Research Environment*; Australian and New Zealand Council for the Care of Animals in Research and Teaching: Glen Osmond, SA, Australia, 1994; pp. 3–18.
11. Mellor, D.J.; Beausoleil, N.J.; Littlewood, K.E.; McLean, A.N.; McGreevy, P.D.; Jones, B.; Wilkins, C. The 2020 Five Domains Model: Including Human–Animal Interactions in Assessments of Animal Welfare. *Animals* **2020**, *10*, 1870. [CrossRef]
12. Mellor, D. Positive Animal Welfare States and Encouraging Environment-Focused and Animal-to-Animal Interactive Behaviours. *N. Z. Vet. J.* **2015**, *63*, 9–16. [CrossRef]
13. Coe, J.C. Naturalizing Habitats for Captive Primates. *Zoo Biol.* **1989**, *8*, 117–125. [CrossRef]
14. Frederick, C.; Fernandes, D. Behavioral Changes in Pottos (*Perodicticus potto*): Effects of Naturalizing an Exhibit. *Int. J. Primatol.* **1996**, *17*, 389–399. [CrossRef]
15. Keulartz, J. Towards a Futureproof Zoo. *Animals* **2023**, *13*, 998. [CrossRef]
16. de Azevedo, C.S.; Cipreste, C.F.; Pizzutto, C.S.; Young, R.J. Review of the Effects of Enclosure Complexity and Design on the Behaviour and Physiology of Zoo Animals. *Animals* **2023**, *13*, 1277. [CrossRef]
17. Williams, E.; Cabana, F.; Nekaris, K.a.I. Improving Diet and Activity of Insectivorous Primates in Captivity: Naturalizing the Diet of Northern Ceylon Gray Slender Loris, *Loris lydekkerianus nordicus*. *Zoo Biol.* **2015**, *34*, 473–482. [CrossRef]
18. Padrell, M.; Amici, F.; Córdoba, M.P.; Llorente, M. Cognitive Enrichment in a Social Setting: Assessing the Use of a Novel Food Maze in Sanctuary-Housed Chimpanzees. *Primates* **2022**, *63*, 509–524. [CrossRef]
19. Clark, F.E.; Gray, S.I.; Bennett, P.; Mason, L.J.; Burgess, K.V. High-Tech and Tactile: Cognitive Enrichment for Zoo-Housed Gorillas. *Front. Psychol.* **2019**, *10*, 1574. [CrossRef] [PubMed]
20. Zhang, Z.; Gao, L.; Zhang, X. Environmental Enrichment Increases Aquatic Animal Welfare: A Systematic Review and Meta-Analysis. *Rev. Aquac.* **2022**, *14*, 1120–1135. [CrossRef]
21. Neal Webb, S.J.; Hau, J.; Schapiro, S.J. Does Group Size Matter? Captive Chimpanzee (*Pan troglodytes*) Behavior as a Function of Group Size and Composition. *Am. J. Primatol.* **2019**, *81*, e22947. [CrossRef]
22. Fultz, A.; Yanagi, A.; Breaux, S.; Beaupre, L. Aggressive, Submissive, and Affiliative Behavior in Sanctuary Chimpanzees (*Pan troglodytes*) During Social Integration. *Animals* **2022**, *12*, 2421. [CrossRef]
23. Ross, S.R. Chimpanzee Welfare in the Context of Science, Policy, and Practice. In *Chimpanzees in Context*; University of Chicago Press: Chicago, IL, USA, 2020; pp. 552–582.
24. Pascual, A.; Kalcher-Sommersguter, E.; Riba, D.; Crailsheim, D. Long-Term Assessment of Captive Chimpanzees: Influence of Social Group Composition, Seasonality and Biographic Background. *Animals* **2023**, *13*, 424. [CrossRef] [PubMed]
25. Abbott, D.H.; Keverne, E.B.; Bercovitch, F.B.; Shively, C.A.; Mendoza, S.P.; Saltzman, W.; Snowdon, C.T.; Ziegler, T.E.; Banjevic, M.; Garland, T.; et al. Are Subordinates Always Stressed? A Comparative Analysis of Rank Differences in Cortisol Levels among Primates. *Horm. Behav.* **2003**, *43*, 67–82. [CrossRef] [PubMed]
26. Ross, S.R.; Bloomsmith, M.A.; Bettinger, T.L.; Wagner, K.E. The Influence of Captive Adolescent Male Chimpanzees on Wounding: Management and Welfare Implications. *Zoo Biol.* **2009**, *28*, 623–634. [CrossRef] [PubMed]
27. Alford, P.L.; Bloomsmith, M.A.; Keeling, M.E.; Beck, T.F. Wounding Aggression during the Formation and Maintenance of Captive, Multimale Chimpanzee Groups. *Zoo Biol.* **1995**, *14*, 347–359. [CrossRef]
28. Takahata, Y. Social Relationships among Adult Males. In *The Chimpanzees of the Mahale Mountains*; Nishida, T., Ed.; University Tokyo Press: Tokyo, Japan, 1990; pp. 148–170.
29. Nishida, T. A Quarter Century of Research in the Mahale Mountains: An Overview. *Chimpanzees Mahale Mt. Sex. Life Hist. Strateg.* **1990**, 3–35.
30. Goodall, J. The Chimpanzees of Gombe: Patterns of Behavior. *J. Trop. Ecol.* **1986**, *3*, 190–191. [CrossRef]
31. Lehmann, J.; Boesch, C. To Fission or to Fusion: Effects of Community Size on Wild Chimpanzee (*Pan troglodytes verus*) Social Organisation. *Behav. Ecol. Sociobiol.* **2004**, *56*, 207–216. [CrossRef]
32. Matsumoto-Oda, A. Behavioral Seasonality in Mahale Chimpanzees. *Primates* **2002**, *43*, 103–117. [CrossRef] [PubMed]
33. Wrangham, R.W.; Smuts, B.B. Sex Differences in the Behavioural Ecology of Chimpanzees in the Gombe National Park, Tanzania. *J. Reprod. Fertil. Suppl.* **1980**, *28*, 13–31.
34. Isabirye-Basuta, G. Food Competition Among Individuals in a Free-Ranging Chimpanzee Community in Kibale Forest, Uganda. *Behaviour* **1988**, *105*, 135–147. [CrossRef]
35. Sakura, O. Factors Affecting Party Size and Composition of Chimpanzees (*Pan troglodytes verus*) Bossou, Guinea. *Int. J. Primatol.* **1994**, *15*, 167–183. [CrossRef]
36. Chapman, C.A.; Chapman, L.J.; Wrangham, R.W. Ecological Constraints on Group Size: An Analysis of Spider Monkey and Chimpanzee Subgroups. *Behav. Ecol. Sociobiol.* **1995**, *36*, 59–70. [CrossRef]
37. Halperin, S. Temporary Association Patterns in Free Ranging Chimpanzees: An Assessment of Individual Grouping Preferences. In *The Great Apes*; Hamburg, D.A., Mccown, E.R., Eds.; Benjamin Cummings: San Francisco, CA, USA, 1979; pp. 491–499.
38. Boesch, C. Social Grouping in Taï Chimpanzees. In *Great Ape Societies*; McGrew, W.C., Marchant, L.F., Nishida, T., Eds.; Cambridge University Press: Cambridge, UK, 1996; pp. 101–113.
39. Ghiglieri, M. *The Chimpanzees of the Kibale Forest*; Columbia University Press: New York, NY, USA, 1984.

40. Boesch, C.; Boesch, H. *The Chimpanzees of the Taï Forest*; Oxford University Press: Oxford, UK, 2000.
41. TAG AZAA. Chimpanzee (Pan troglodytes) Care Manual Silver Spring. MD Assoc. *Zoos Aquar.* 2010. Available online: https://assets.speakcdn.com/assets/2332/chimpanzeecaremanual2010r.pdf (accessed on 16 February 2023).
42. National Institutes of Health (NIH). *Council of Councils Working Group on the Use of Chimpanzees in NIH-Supported Research*; Council of Councils Working Group; Final Report; National Institutes of Health: Bethesda, MD, USA, 2013.
43. Llorente, M.; Riba, D.; Ballesta, S.; Feliu, O.; Rostán, C. Rehabilitation and Socialization of Chimpanzees (*Pan troglodytes*) Used for Entertainment and as Pets: An 8-Year Study at Fundació Mona. *Int. J. Primatol.* **2015**, *36*, 605–624. [CrossRef]
44. Lehmann, J.; Korstjens, A.H.; Dunbar, R.I.M. Group Size, Grooming and Social Cohesion in Primates. *Anim. Behav.* **2007**, *74*, 1617–1629. [CrossRef]
45. Morin, P.A. Reproductive Strategies in Chimpanzees. *Am. J. Phys. Anthropol.* **1993**, *36*, 179–212. [CrossRef]
46. Herbinger, I.; Papworth, S.; Boesch, C.; Zuberbühler, K. Vocal, Gestural and Locomotor Responses of Wild Chimpanzees to Familiar and Unfamiliar Intruders: A Playback Study. *Anim. Behav.* **2009**, *78*, 1389–1396. [CrossRef]
47. Wilson, M.L.; Kahlenberg, S.M.; Wells, M.; Wrangham, R.W. Ecological and Social Factors Affect the Occurrence and Outcomes of Intergroup Encounters in Chimpanzees. *Anim. Behav.* **2012**, *83*, 277–291. [CrossRef]
48. Watts, D.; Mitani, J. Boundary Patrols and Intergroup Encounters in Wild Chimpanzees. *Behaviour* **2001**, *138*, 299–327. [CrossRef]
49. Goodall, J.; Bandura, A.; Bergmann, E.; Busse, C.; Matam, H.; Mpongo, E.; Pierce, A.; Riss, D. Inter-Community Interactions in the Chimpanzee Populations of the Gombe National Park. In *The Great Apes*; Benjamin/Cummings: Menlo Park, CA, USA, 1979; pp. 13–53.
50. Mitani, J.C.; Watts, D.P.; Amsler, S.J. Lethal Intergroup Aggression Leads to Territorial Expansion in Wild Chimpanzees. *Curr. Biol.* **2010**, *20*, R507–R508. [CrossRef]
51. Reynolds, V. *Budongo: A Forest and Its Chimpanzees*; Methuen & Co: London, UK, 1965.
52. Boesch, C.; Crockford, C.; Herbinger, I.; Wittig, R.; Moebius, Y.; Normand, E. Intergroup Conflicts among Chimpanzees in Taï National Park: Lethal Violence and the Female Perspective. *Am. J. Primatol.* **2008**, *70*, 519–532. [CrossRef]
53. Watts, D.P.; Muller, M.; Amsler, S.J.; Mbabazi, G.; Mitani, J.C. Lethal Intergroup Aggression by Chimpanzees in Kibale National Park, Uganda. *Am. J. Primatol.* **2006**, *68*, 161–180. [CrossRef] [PubMed]
54. Neal Webb, S.J.; Hau, J.; Lambeth, S.P.; Schapiro, S.J. Differences in Behavior Between Elderly and Nonelderly Captive Chimpanzees and the Effects of the Social Environment. *J. Am. Assoc. Lab. Anim. Sci.* **2019**, *58*, 783–789. [CrossRef] [PubMed]
55. Grand, A.P.; Leighty, K.A.; Cory, L.J.; Maloney, M.A.; Phillips, R.S.; Bettinger, T.L. The Neighbor Effect in Bachelor and Breeding Groups of Western Lowland Gorillas (*Gorilla gorilla gorilla*). *Int. J. Comp. Psychol.* **2013**, *26*, 26–36. [CrossRef]
56. Videan, E.N.; Fritz, J.; Schwandt, M.; Howell, S. Neighbor Effect: Evidence of Affiliative and Agonistic Social Contagion in Captive Chimpanzees (*Pan troglodytes*). *Am. J. Primatol.* **2005**, *66*, 131–144. [CrossRef] [PubMed]
57. Gil-Dolz, J.; Riba, D.; Crailsheim, D. Neighbors Matter: An Investigation into Intergroup Interactions Affecting the Social Networks of Adjacent Chimpanzee Groups. *Ecologies* **2023**, *4*, 385–405. [CrossRef]
58. Crailsheim, D. Welfare Promoting Environments: Assessment and Management in Sanctuary Chimpanzees. Ph.D. Thesis, Universitat de Girona, Girona, Spain, 2024.
59. Llorente, M.; Riba, D.; Mosquera, M.; Ventura, M.; Feliu, O. Hunting Activity among Naturalistically Housed Chimpanzees (*Pan troglodytes*) at the Fundació Mona (Girona, Spain). Predation, Occasional Consumption and Strategies in Rehabilitated Animals. *Animals* **2012**, *2*, 363–376. [CrossRef] [PubMed]
60. Cano, R. Use of Natural Resources by Sanctuary Chimpanzees (*Pan troglodytes*): Understanding the Significance of Naturalistic Environments. Master's Thesis, Hedmark University College, Elverum, Norway, 2014.
61. The Aerial View of Fundació Mona: Centre de Recuperació de Primats [Screenshot from Google Earth]. Available online: https://earth.google.com/web/search/fundacio+MONA/@41.90252999,2.816899,92.20267318a,146.23533157d,35y,103.6530503h,29.18438839t,-0r/data=CigiJgokCX0c22U_ojRAEXwc22U_ojTAGf7xRqD29URAIS97iADcNk7AOgMKATA (accessed on 31 March 2024).
62. Wark, J.D.; Cronin, K.A.; Niemann, T.; Shender, M.A.; Horrigan, A.; Kao, A.; Ross, M.R. Monitoring the Behavior and Habitat Use of Animals to Enhance Welfare Using the ZooMonitor App. *Anim. Behav. Cogn.* **2019**, *6*, 158–167. [CrossRef]
63. Altmann, J. Observational Study of Behavior: Sampling Methods. *Behaviour* **1974**, *49*, 227–266. [CrossRef] [PubMed]
64. Baayen, R. *Analyzing Linguistic Data: A Practical Introduction to Statistics Using R*; Cambridge University Press: Cambridge, UK, 2008.
65. Brooks, M.E.; Kristensen, K.; van Benthem, K.J.; Magnusson, A.; Berg, C.W.; Nielsen, A.; Skaug, H.J.; Machler, M.; Bolker, B.M. glmmTMB Balances Speed and Flexibility among Packages for Zero-Inflated Generalized Linear Mixed Modeling. *R J.* **2017**, *9*, 378–400. [CrossRef]
66. R Core Team. *R: A Language and Environment for Statistical Computing*; R Core Team: Vienna, Austria, 2018.
67. Dobson, A. *An Introduction to Generalized Linear Models*; Chapman and Hall/CRC: Boca Raton, FL, USA, 2002.
68. Barr, D.J.; Levy, R.; Scheepers, C.; Tily, H.J. Random Effects Structure for Confirmatory Hypothesis Testing: Keep It Maximal. *J. Mem. Lang.* **2013**, *68*, 255–278. [CrossRef]
69. Field, A. *Discovering Statistics Using SPSS*; Sage Publications: London, UK, 2009.
70. Lenth, R. Emmeans: Estimated Marginal Means, Aka Least-Squares Means. *R Package Version 1* **2020**, *1*, 8.
71. Goodall, J. Social Rejection, Exclusion, and Shunning among the Gombe Chimpanzees. *Ethol. Sociobiol.* **1986**, *7*, 227–236. [CrossRef]

72. Baker, K.C.; Aureli, F. The Neighbor Effect: Other Groups Influence Intragroup Agonistic Behavior in Captive Chimpanzees. *Am. J. Primatol.* **1996**, *40*, 283–291. [CrossRef]
73. Baker, K.C.; Aureli, F. Behavioural Indicators of Anxiety: An Empirical Test in Chimpanzees. *Behaviour* **1997**, *134*, 1031–1050. [CrossRef]
74. Berthier, J.M.; Semple, S. Observing Grooming Promotes Affiliation in Barbary Macaques. *Proc. R. Soc. B Biol. Sci.* **2018**, *285*, 20181964. [CrossRef]
75. Ostner, J.; Wilken, J.; Schülke, O. Social Contagion of Affiliation in Female Macaques. *R. Soc. Open Sci.* **2021**, *8*, 201538. [CrossRef] [PubMed]
76. Sandars, G. ChimpanSee, ChimpanDo: A Review of the Significance of Social Contagion, and Exploration of Grooming and Play Contagion in Chimpanzees. Master's Thesis, Durham University, Durham, UK, 2022.
77. Samuni, L.; Mielke, A.; Preis, A.; Crockford, C.; Wittig, R.M. Intergroup Competition Enhances Chimpanzee (*Pan troglodytes* Verus) In-Group Cohesion. *Int. J. Primatol.* **2020**, *41*, 342–362. [CrossRef]
78. Romero, T.; de Waal, F.B.M. Chimpanzee (*Pan troglodytes*) Consolation: Third-Party Identity as a Window on Possible Function. *J. Comp. Psychol.* **2010**, *124*, 278–286. [CrossRef] [PubMed]
79. Romero, T.; Castellanos, M.A.; de Waal, F.B.M. Consolation as Possible Expression of Sympathetic Concern among Chimpanzees. *Proc. Natl. Acad. Sci. USA* **2010**, *107*, 12110–12115. [CrossRef]
80. Fraser, O.N.; Aureli, F. Reconciliation, Consolation and Postconflict Behavioral Specificity in Chimpanzees. *Am. J. Primatol.* **2008**, *70*, 1114–1123. [CrossRef]
81. Fraser, O.N.; Stahl, D.; Aureli, F. Stress Reduction through Consolation in Chimpanzees. *Proc. Natl. Acad. Sci. USA* **2008**, *105*, 8557–8562. [CrossRef] [PubMed]
82. Preuschoft, S.; Wang, X.; Aureli, F.; de Waal, F.B.M. Reconciliation in Captive Chimpanzees: A Reevaluation with Controlled Methods. *Int. J. Primatol.* **2002**, *23*, 29–50. [CrossRef]
83. Silk, J.B. The Form and Function of Reconciliation in Primates. *Annu. Rev. Anthropol.* **2002**, *31*, 21–44. [CrossRef]
84. Cordoni, G.; Palagi, E.; Tarli, S.B. Reconciliation and Consolation in Captive Western Gorillas. *Int. J. Primatol.* **2006**, *27*, 1365–1382. [CrossRef]
85. Puga-Gonzalez, I.; Butovskaya, M.; Thierry, B.; Hemelrijk, C.K. Empathy versus Parsimony in Understanding Post-Conflict Affiliation in Monkeys: Model and Empirical Data. *PLoS ONE* **2014**, *9*, e91262. [CrossRef] [PubMed]
86. Palagi, E.; Cordoni, G.; Tarli, S.B. Possible Roles of Consolation in Captive Chimpanzees (*Pan troglodytes*). *Am. J. Phys. Anthropol.* **2006**, *129*, 105–111. [CrossRef] [PubMed]
87. Wittig, R.M.; Boesch, C. Receiving Post-Conflict Affiliation from the Enemy's Friend Reconciles Former Opponents. *PLoS ONE* **2010**, *5*, e13995. [CrossRef] [PubMed]
88. De Waal, F.B.M. *Chimpanzee Cultures*; Wrangham, R.W., McGrew, W.C., De Waal, F.B., Heltne, B.G., Eds.; Harvard University Press: Cambridge, UK, 1996; pp. 243–260.
89. Crailsheim, D.; Stüger, H.P.; Kalcher-Sommersguter, E.; Llorente, M. Early Life Experience and Alterations of Group Composition Shape the Social Grooming Networks of Former Pet and Entertainment Chimpanzees (*Pan troglodytes*). *PLoS ONE* **2020**, *15*, e0226947. [CrossRef]
90. Padrell, M.; Riba, D.; Úbeda, Y.; Amici, F.; Llorente, M. Personality, Cognition and Behavior in Chimpanzees: A New Approach Based on Eysenck's Model. *PeerJ* **2020**, *8*, e9707. [CrossRef] [PubMed]
91. Leavens, D.A.; Aureli, F.; Hopkins, W.D.; Hyatt, C.W. Effects of Cognitive Challenge on Self-Directed Behaviors by Chimpanzees (*Pan troglodytes*). *Am. J. Primatol.* **2001**, *55*, 1–14. [CrossRef]
92. Yamanashi, Y.; Matsuzawa, T. Emotional Consequences When Chimpanzees (*Pan troglodytes*) Face Challenges: Individual Differences in Self-Directed Behaviours during Cognitive Tasks. *Anim. Welf.* **2010**, *19*, 25–30. [CrossRef]
93. Kutsukake, N. Assessing Relationship Quality and Social Anxiety Among Wild Chimpanzees Using Self-Directed Behaviour. *Behaviour* **2003**, *140*, 1153–1171. [CrossRef]
94. Ferdowsian, H.R.; Durham, D.L.; Kimwele, C.; Kranendonk, G.; Otali, E.; Akugizibwe, T.; Mulcahy, J.B.; Ajarova, L.; Johnson, C.M. Signs of Mood and Anxiety Disorders in Chimpanzees. *PLoS ONE* **2011**, *6*, e19855. [CrossRef] [PubMed]
95. Botero, M.; MacDonald, S.E.; Miller, R.S. Anxiety-Related Behavior of Orphan Chimpanzees (*Pan troglodytes* Schweinfurthii) at Gombe National Park, Tanzania. *Primates* **2013**, *54*, 21–26. [CrossRef] [PubMed]
96. Koski, S.E.; Koops, K.; Sterck, E.H.M. Reconciliation, Relationship Quality, and Postconflict Anxiety: Testing the Integrated Hypothesis in Captive Chimpanzees. *Am. J. Primatol.* **2007**, *69*, 158–172. [CrossRef] [PubMed]
97. Lopresti-Goodman, S.M.; Kameka, M.; Dube, A. Stereotypical Behaviors in Chimpanzees Rescued from the African Bushmeat and Pet Trade. *Behav. Sci.* **2013**, *3*, 1–20. [CrossRef] [PubMed]
98. Mason, G.J.; Cooper, J.; Clarebrough, C. Frustrations of Fur-Farmed Mink. *Nature* **2001**, *410*, 35–36. [CrossRef] [PubMed]
99. DeBoer, S.P.; Garner, J.P.; McCain, R.R.; Lay, D.C.; Eicher, S.D.; Marchant-Forde, J.N. An Initial Investigation into the Effects of Isolation and Enrichment on the Welfare of Laboratory Pigs Housed in the PigTurn®System, Assessed Using Tear Staining, Behaviour, Physiology and Haematology. *Anim. Welf.* **2015**, *24*, 15–27. [CrossRef]
100. Kawanaka, K. Age Differences in Spatial Positioning of Males in a Chimpanzee Unit-Group at the Mahale Mountains National Park, Tanzania. *Primates* **1993**, *34*, 255–270. [CrossRef]

101. Riopelle, A.; Rogers, C. Age Changes in Chimpanzees. In *Behavior of Nonhuman Primates: Modern Research Trends*; Academic Press: New York, NY, USA, 1965; pp. 449–462.
102. Fuentes, A.; Malone, N.; Sanz, C.; Matheson, M.; Vaughan, L. Conflict and Post-Conflict Behavior in a Small Group of Chimpanzees. *Primates* **2002**, *43*, 223–235. [CrossRef]