

Visitor impacts on social dynamics and space use in captive Western lowland gorillas (*Gorilla gorilla gorilla*) in a naturalistic zoo exhibit: A new methodological approach

Hugo Leroy^{a,*}, Calogero Montedoro^a, Jean-Pascal Guery^b, Thierry Hance^a

^a Earth and life Institute, Biodiversity Research Centre UCL, L7.07.04, Croix du Sud, 4-5, Louvain-la-Neuve b-1348, Belgium

^b La Vallée des Singes. Le Gureau, Romagne 86700, France

ARTICLE INFO

Keywords:

Western lowland gorilla
Human-animal interactions
Naturalistic zoo exhibit
Ripley's function
Visitor effect
Zoo animal welfare

ABSTRACT

The welfare of zoo animals has come under increasing scrutiny, yet the effects of visitors on captive species, particularly in relation to environmental factors and individual variability, remain insufficiently studied. This study introduces a novel methodology to assess how visitors influence the social and spatial dynamics of Western lowland gorillas (*Gorilla gorilla gorilla*) in naturalistic enclosures. We conducted daily observation sessions to track the positioning of gorillas relative to one another and their environment. Key visitor-related factors such as mere presence, density, movement and activity along two independent paths, adjacent to the enclosure were recorded and related to the gorillas' spatial distribution. Two indices – the Retreat Index (RI) and the Exposure Tolerance Index (ETI) – were developed to quantify each individual's tendency to retreat from exposed areas or tolerate visitor observation. For the first time, Ripley's functions were employed to assess changes in distribution patterns among individuals in response to visitor presence. Our results show that visitor pressure significantly reduces inter-individual distances, a trend further amplified by environmental factors such as wind, temperature, and humidity. Among visitor-related variables, movement of new visitors, rather than mere presence or crowd size, was the primary factor triggering behavioural changes. Social network analysis revealed increased interactions, particularly between females and their offspring, along with enhanced comfort and resting behaviours in the presence of visitors. Additionally, we observed a dichotomy in the gorillas' behavioural response, with less pronounced reactions in areas where visitors were less visible. Ripley's functions identified substantial aggregation of gorillas in visitor-influenced scenarios, in contrast to a near-random distribution when visitors were absent. This pilot study establishes a foundation for developing a comprehensive methodology, applicable across various zoo settings, to evaluate the impact of visitor-induced disturbances on gorillas, offering fresh insights into the welfare of captive animals.

1. Introduction

In recent decades, zoo housing conditions have evolved considerably, moving from rudimentary enclosures towards more complex environments that better replicate natural habitats (Carter et al., 2015), promoting natural behaviours (Quick, 1984; Maple and Finlay, 1989) and enhancing the 'zoo experience' (Hosey, 2005). Despite these advancements, our understanding of social structures and space utilisation within 'naturalistic' primate enclosures remains limited, especially regarding the potential influence of zoo visitors (Hosey, 2005). Western lowland gorillas (*Gorilla gorilla gorilla*), one of the most iconic species in zoological institutions (Carr, 2016), provide a particularly relevant

model for such investigations. Being predominantly terrestrial (Ogden et al., 1993; Ross and Lukas, 2006) and possessing a complex social structure, gorillas are frequently exposed to large numbers of visitors (Moss and Esson, 2010), making them an ideal species to examine the potential effects of human presence on their behaviour. Previous research on captive primates has highlighted a range of behavioural responses to visitors, including increased aggression and reduced affiliative or exploratory behaviours (Blaney and Wells, 2004; Wells, 2005). However, these studies often focus on specific aspects such as the mere presence or absence of visitors (Chamove et al., 1988; Williams et al., 2022), visitor density (see Glatston et al., 1984), or visitor activity (Hosey and Druck, 1987) and examine animal behaviour in response to

* Correspondence to: Earth and Life Institute, Biodiversity Research Centre, UCLouvain, L7.07.04, Croix du Sud, 4-5, Louvain la-Neuve b-1348, Belgium
E-mail address: leroyhugo@gmail.com (H. Leroy).

<https://doi.org/10.1016/j.applanim.2024.106433>

Received 12 August 2024; Received in revised form 15 October 2024; Accepted 28 October 2024

Available online 9 November 2024

0168-1591/© 2024 Elsevier B.V. All rights are reserved, including those for text and data mining, AI training, and similar technologies.

these specific variations. This narrow scope makes it difficult to extrapolate findings and fully comprehend the complexity of behavioural responses, which are sometimes described as positive, negative, or neutral. For example, Wells (2005) reported that lower visitor density correlated with relaxed behaviour and increased resting or nesting, while higher densities were associated with aggression and stereotypic behaviour.

One of the main challenges in studying the effects of visitors on captive animals lies in the variability of environmental conditions and group structures across zoological institutions. Existing methodologies often fail to capture the intricate interactions between visitors, the environment, and the animals. While behavioural changes in response to visitors are observed, it is difficult to ascertain whether these changes are directly due to visitor presence or other confounding factors such as temperature, social dynamics, or hormonal fluctuations. Behavioural responses can also vary according to individual personality, complicating the generalisation of results. It is therefore essential to consider these elements simultaneously within the same analysis, especially as it is common to attribute to visitors what is in fact only due to the environment or the time of day (Goodenough et al., 2019). Animal perception of visitors is another often-overlooked aspect in studies of human-animal interactions. Within a single group, individual perceptions of visitors may differ, influencing both individual behaviours and the group's social and spatial structure. For instance, some gorillas may perceive visitors as stressors and seek less exposed areas, while others may display curiosity or indifference. These differences in tolerance for visitor visibility add further complexity to the analysis of visitor impacts.

To address these limitations, this study proposes a more integrative approach to understanding the interactions between captive gorillas and zoo visitors. The framework we present aims to provide a more nuanced and precise assessment of visitor effects by simultaneously considering various factors that influence gorilla behaviour. Key factors include social elements such as parturition, which influences female interactions (Stoinski et al., 2003), dietary composition, which plays a crucial role in the genesis of interactions (Flohic et al., 2015), and castration, which has been shown to promote closer and more positive group interactions (Létang et al., 2021). Additionally, environmental variables such as temperature and humidity significantly affect spatial distribution, independent of visitor presence. For example, Rose et al. (2020) found that temperature outweighed visitor presence in predicting enclosure use in Black-helmeted Hornbills (*Ceratogymna atrata*). By integrating these variables into the analysis, we can better isolate the specific effects of visitors on gorilla behaviour.

Animal perception of visitors is a focal point of this study. Previous research has highlighted factors such as visitor viewing height (Chamove et al., 1988), direct visual contact (Blaney and Wells, 2004), and the possibility for animals to move away (Cairo-Evans et al., 2022) as key influences on primate behaviour. We hypothesise that differing perceptions of visitors will affect not only individual behaviour but also the broader social and spatial structure of the troop. To explore this hypothesis, we examine various visitor-related variables such as presence or absence, density, movement, and activity, assessing their respective impacts on gorilla behaviour. Our approach aligns with findings from Lewis et al. (2020), who demonstrated that direct visitor density is a better predictor of individual behavioural changes than daily zoo entry numbers. Moreover, we account for the individual personality traits of each gorilla in our analysis to gain a more objective understanding of behavioural responses to visitors, following the protocol introduced by Gold and Maple (1994).

This study is divided into two main components: social and spatial. The social component aims to assess how visitors affect gorillas' social structures through a comprehensive Social Network Analysis (SNA), focusing on proximity and contact between individuals, the shifting importance of each gorilla within the troop, the modelling of inter-individual distances, and the type of social interactions. For the spatial component, the enclosure was divided into two types of zones:

'proximal', where individuals are visible to visitors, and 'distal', where they always remain out of sight. By counting gorilla presence in these two types of zones and correlating this with data on visitor presence or absence, we developed two indices. These indices quantify each gorilla's tolerance to being observed by visitors and identify zones where visitor presence does or does not trigger a behavioural response. This approach will complement the methodology and allow for an explanation of individual variability in the 'visitor effect' that cannot be captured at the group level.

More conventional indices, such as relative variance, aggregation, Lexis, or Charlier, could be used to analyse dispersion. However, de Freitas Alves and de Santana, (2022) highlight that these methods do not account for distribution differences at varying scales. Additionally, methods based on nearest-neighbour distances, like the Clark-Evans index (Clark and Evans, 1954), are limited to 'the very fine scale of nearest neighbours' spatial structure (Dale et al., 2002) and restrict broader interpretations in cases of wide dispersal. Kint et al. (2003) further indicate that the CE index is relevant only for distributions presumed aggregated prior to analysis. Thus, we chose to adapt Ripley's functions for individual-level analysis of gorilla spatial dispersal. Ripley's K function is commonly employed to assess spatial point patterns, considering distances among all individuals rather than just nearest neighbours. It facilitates hypothesis testing, parameter estimation, and model fitting in both univariate and multivariate contexts across various spatial scales (Szmyt, 2014). Traditionally used in spatial ecology, Ripley's K has primarily focused on static phenomena, such as trees or climatic events (Lynch and Moorcroft, 2008; Turner, 2009; Law et al., 2009; Kiskowski et al., 2009). To our knowledge, this marks the first application of these functions to the spatial dynamics of mobile animal species. By treating mobile events (gorilla observations) as fixed points under specific conditions, such as visitor presence, and recording data at regular intervals, this innovative approach reveals global dispersion patterns. In a controlled setting with defined spaces and high visibility, Ripley's functions offer critical insights into dispersal patterns and group dynamics at both fine and broad scales.

In sum, this study aims to establish a comprehensive methodology for evaluating the effects of visitors on captive animals, focusing specifically on gorillas. By accounting for environmental, social, and individual variability, our approach offers a deeper understanding of animal-visitor interactions, which can be adapted for use in most zoos, contributing to improved management practices in captivity.

2. Material and methods

2.1. Model and study site

This study was conducted on a troop of 10 Western lowland gorillas (*Gorilla gorilla gorilla*). The group is a stable and cohesive harem, in line with the standards for reproductive groups in captivity set by the EAZA Best Practice Guidelines (2024 edition) and is consistent with the median troop size observed in wild gorillas (Parnell, 2002; Yamagiwa et al., 2003). The troop consists of a silverback, four adult females, and their offspring (see Table 1). Notably, the troop also includes two adult and sub-adult males who have been castrated, in accordance with the European Endangered Species Programme (EEP), to maintain a balanced sex ratio and ensure genetic diversity (Vermeer et al., 2014). Few studies have examined the impact of this hormonal upheaval in gorillas, despite its potential to significantly affect the social structure of the troop, and even fewer have considered the effect of visitors on these individuals. This factor was therefore included in the present study. Previous research has indicated that castrated males, compared to intact ones, engage in more positive interactions and exhibit greater cohesion (Létang et al., 2021) without significant changes to their morphology, apart from secondary sexual characteristics (Torres et al., 2022). This helps facilitate their acceptance by the silverback and reduces underlying tensions within the troop.

Table 1Composition and characteristics of the Western lowland gorilla (*Gorilla gorilla gorilla*) troop at La Vallée des Singes (France).

Name	Sex	Age (years) when the study began (06/2022)	Age class	Year of birth	Kinship	Sterilization/contraception
Virunga (Vi)	F	51	Ad	1971	-	-
Yaounde (Ya)*	M	38	Ad	1983	Father Maw, Djo, Ko, Ivi, Ba	-
Moseka (Mo)	F	38	Ad	1984	Mother Djo, Maw, Ko	Implant
Djomo (Djo)	M	13	Ad	2008	Brother Maw, Ko	Castrated
Mawete (Maw)	M	10	Sub – Ad	2011	Brother Djo, Ko	Castrated
Mah-Mah (Ma)	F	19	Ad	2002	Mother Ba	Pill
Hakuna (Ha)	F	26	Ad	1996	Mother Ivi	Pill
Kouam (Ko)	M	6	Inf	2016	Brother Djo, Ma	-
Ivindo (Ivi)	F	4	Inf	2017	-	-
Basoko (Ba)	M	2	Inf	2020	-	-

Ad adult (females > 8 years, males > 12 years), Sub-Ad sub-adult (females 6–8 years, males 6–12 years), Inf infants (0–6 years), M males, F females, Yaounde (Ya) the dominant silverback has been highlighted in bold followed by a *.

The troop is housed at La Vallée des Singes in the Vienne region of France (Romagne), one of the few zoos in Europe dedicated exclusively to primates. Over time, this park has become a reference for ex-situ primate research, thanks to its cage-free layout, naturalistic enclosures, and minimal interaction between primates and caretakers. The gorillas were observed in their outdoor enclosure, a predominantly wooded, naturalistic island covering approximately 3700 m², with no structural enrichment and surrounded by a canal filled with water. The enclosure also includes indoor lodges of around 150 m², although the gorillas did not have access to these during the observation period. Water was available ad libitum, and the gorillas were fed during public sessions four times a day in the summer season (May to August) at 11:15, 14:00, 15:30, and 17:00.

The Fig. 1 defines the boundaries of the different zones used in the study. The visitor zones correspond to the two paths on either side of the enclosure from which visitors can observe the gorillas. Proximal zones 1 and 2 correspond to the part of the enclosure where the gorillas can be seen by visitors present in visitor zones 1 (V1) and 2 (V2) respectively. The distal, more central zone corresponds to the area from which it is impossible for visitors to see the gorillas, no matter where they are on the paths. Illustrations have been added to facilitate the reader's perception of the visitors' possible view of the gorillas and enclosure, as well as the gorillas' view of the areas accessible to visitors.

2.2. Data collection

2.2.1. Data related to gorillas

In order to correlate environmental variables and those associated with visitors to the gorilla distribution, we recorded the exact position (coordinates) of all the gorillas within their enclosure at regular time intervals. Based on these coordinates, we focused on the variation in distance between all individuals, specific interest groups, and on the probability of the gorillas' presence within the three defined zones of the territory (i.e. the two "proximal zones" at the periphery, and the "distal zone" at the centre of the enclosure, see Fig. 1). We hypothesised that visitor-induced disturbances would prompt the gorillas to avoid them, resulting in a higher frequency of gorilla presence in the distal zone, which would act as a "retreat area" as described by Anderson et al. (2002) or Cairo-Evans et al. (2022). Although it is difficult to precisely estimate the parts of the territory where gorillas cannot see the visitors, we assume that this overlaps with the area where the gorillas are never visible to visitors, defined here as the "distal zone". If this retreat behaviour is confirmed, it should lead to an overall spatial contraction of the troop in the presence of visitors due to a reduction in the space utilised. As a result, we would expect to observe a decrease in the distance between individuals, as well as fewer occurrences of gorillas in the proximal zones. To minimise interference between the sole observer and the gorillas, observations were conducted from the rooftop of the night lodges (see Fig. 1), which offered a comprehensive view of the entire area. To maximise the contrast between the presence and absence of

visitors within the same time frame, data collection took place during the high tourist season, from 30/07/2022–05/09/2022. The position of all individuals was recorded on a base map by screening at regular five-minute intervals, with four daily observation sessions (see schedule in Table 2), totaling ten screenings per session. To account for the effect of the time of day on gorilla behaviour, observation sessions were repeated in the morning and afternoon, both in the presence and absence of visitors, and were close enough together to capture transitions, such as the arrival or departure of visitors. During the specified period, a total of (n=5357) observation points were collected across (n=722) screenings of all individuals' positions.

All data points mapped were georeferenced using the Geographic Information System (GIS) QGIS. From the resulting distance matrices, the following values were calculated for each observation session:

- Average distance between all individuals (ADI)
- Average distance between the silverback and the other sub-adult/castrated adult males (SBM)
- Average distance between the silverback and the females (DSF)
- Average distance between females (DAF)
- Average distance between females and their offspring (DFY)

When two or more individuals were observed in direct contact, the type of interaction was recorded to determine any potential differences in behaviour depending on the presence or absence of visitors. Eight interaction types were distinguished and listed in Table 3.

With the individuals' positions known, for each observation we were able to calculate:

- The number of individuals present in zone P1 (NP1)
- The number of individuals present in zone P2 (NP2)
- The number of individuals present in the distal zone (NDis)
- The number of occurrences in each of the zones for each of the individuals (NT)

2.2.2. Data related to visitors

In previous studies that quantified the number of visitors around enclosures, only visitor density or position was typically considered (see, for example, Glatston et al., 1984, Chamove et al., 1988, Lewis et al., 2020). To more accurately capture visitor-specific variables, two cameras were used to record both visitor areas (see V1 and V2 in Fig. 1). After each day of sampling, the recorded footage was processed to extract the following values (n = 120 hours of recording):

- **V1T/V2T**: The number of visitors present in each zone at the time the gorillas' positions were recorded.
- **V1Max/V2Max**: The maximum number of visitors present simultaneously in each zone during the 5-minute interval between two recordings, i.e., 5 minutes before each localisation point was marked

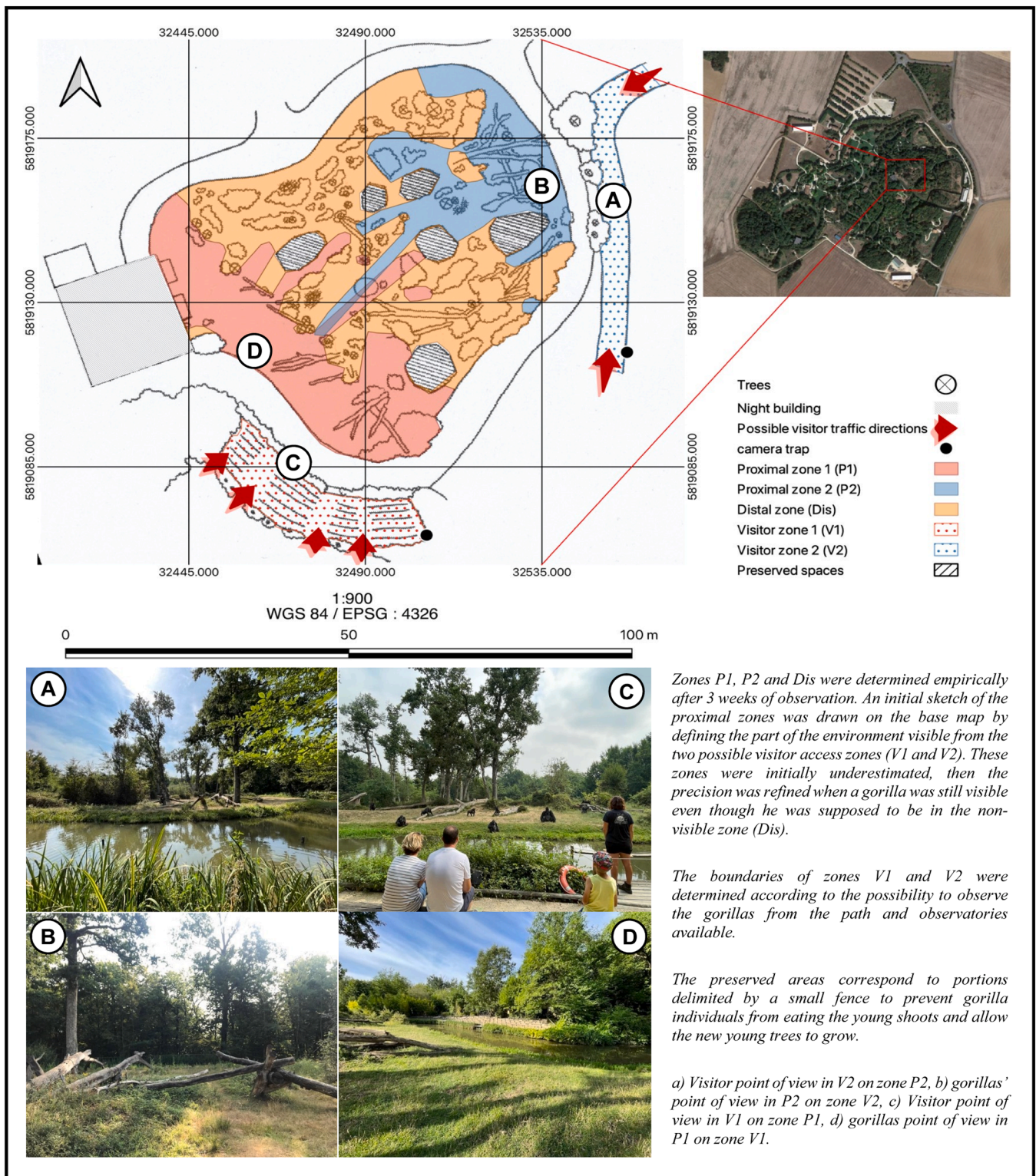


Fig. 1. Diagram of the gorilla enclosure at La Vallée des Singes (France) showing the areas used for study and illustration of the different viewpoints.

(this also includes a measurement taken 5 minutes before the first point of each session was collected).

- **V1N/V2N:** The number of new visitors passing through visitor zones V1 and V2 during the 5-minute interval between two measurements.
- **V1i/V2i:** The type of crowd present during the 5-minute interval between two measurements (categorised as either active or passive, with 'active' indicating at least one visitor attempting to interact directly with a gorilla using words or gestures).

It is important to note that during video recording, the cameras were positioned to capture as few identifiable faces as possible, or filmed from a distance where identification was not feasible. At no point was personal data collected from visitors, and all video footage was discarded after processing the relevant data. The video equipment was clearly visible to visitors and labelled as part of an experimental setup recording the pathway. Given the transparent casing of the device, visitors were even able to see the cameras themselves. No complaints or negative

Table 2
Planning of sampling sessions.

For each sampling day	
Visitor present	Visitor absent
Morning session	Morning session
10: 20 – 11: 10 AM	09: 30 – 10: 20 AM
Afternoon session	Afternoon session
03: 50 – 04: 40 PM	05: 10 – 06: 00 PM

For the two afternoon sessions, each observation was spaced at least 10 minutes apart from the public feeding, to give the gorillas time to resume normal activity and disperse back into their enclosure.

Table 3
Ethogram of observed social interaction types among gorillas at La Vallée des Singes (France).

Behaviour Type	Description
Eating together	At least two individuals feeding on the same branch placed in the enclosure by a caretaker.
Breastfeeding	An adult female breastfeeding one of the troop's infants.
Fighting	Any agonistic behaviour (e.g. hitting, chasing, or pinching).
Grooming	Comfort behaviours, either mutual or directed (e.g. rubbing, lounging, embracing, or delousing).
Manipulating traps	Interaction with ladders controlling access to inner lodges, attempting to open or strike the traps.
Moving	One individual carrying another as they move through the enclosure.
Playing	Play-related behaviours (e.g. chasing, wrestling, spinning, or tickling).
Resting	At least two individuals sitting or lying down together without engaging in other comfort behaviours. Neither is asleep.
Sleeping	At least two individuals lying next to or on top of each other while asleep.

In cases of direct contact, a single point was marked on the physical map to speed up measurement. However, two superimposed points were placed on QGIS, each with a unique ID for clarity and analysis, with a maximum distance of 0.01 m between the points to represent the direct contact digitally.

feedback were reported throughout the entire study. The positioning and field of view of the cameras are shown in Fig. 1.

The V1i/V2i values were not included in the analysis because of the limited number of corresponding observations ($n = 7/722$) and the fact that no radical change in behaviour was observed as a result of this interaction. However, we considered it relevant to describe this in the methodology because noise disturbance has already been described as potentially affecting spatial distribution (see Lewis et al., 2020).

2.2.3. Data related to the environment

Temperature, rain, or strong gusts of wind could significantly reduce the presence of individuals in proximal zones, which are more exposed to climatic disturbances than the distal zone. This may influence the structure of the social network by affecting inter-individual distances and altering spatial distribution. To account for these climatic fluctuations during each observation session of the gorilla troop, we collected the corresponding climate data.

These data were collected using 3 HOBO data loggers ("Temperature/Light 64 K Data Logger") placed in fixed locations (on the roof of the building and in two shaded areas inaccessible to visitors) and averaged to obtain temperature data. To complement these measurements, data from three nearby weather stations (BRUX; 46°16'32.0 "N 0°11'25.0 "E, CIVRAY; 46°09'37.0 "N 0°17'55.0 "E and LUSIGNAN; 46°25'04.0 "N 0°07'10.0 "E) were averaged to obtain values for relative humidity (RH%), wind speed (km/h), and precipitation (mm).

Rainfall data were excluded from the analysis because the study period was exceptionally dry, with only three recorded rain events, representing just 0.1 mm of rainfall.

3. Data analysis

3.1. Structure of the social network and Nature of interaction

3.1.1. Inter-individual distances models

To analyse inter-individual distances, Generalised Linear Models (GLMs) were applied, using the distance classes described earlier (ADI, SBM, DSF, DAF, and DFY) as response variables. These models accounted for the various visitor-related factors in the two zones (V1 and V2) and their interactions, alongside environmental variables and the time of day. The day of observation was included as a random factor to account for repeated observations of the same group of individuals. Some response variables exhibited slight asymmetry with a straight tail, but the QQ plot and mean-to-median deviations indicated acceptable symmetry. Consequently, either a Gaussian or Gamma distribution was employed to model the count data.

3.1.2. Social network analysis (SNA)

A detailed social network analysis (SNA) is essential for understanding how visitors affect the social structure and interactions between individuals. To construct these networks, graphs were created where each gorilla is represented by a point (node), and interactions between them are represented by links. We employed undirected links for symmetrical interactions, as opposed to asymmetrical interactions where the action is directed from one individual to another (e.g., "follows", "hits", "influences"). The aim was to graphically represent the Strength of interactions between each gorilla. Each link was assigned a "weight", corresponding to a commonly used value in this type of SNA analysis: the Simple Ratio Index (SRI; Rose and Croft, 2015).

The SRI between two individuals, a and b, is calculated as follows:

$$SRI = \frac{x}{(x + Yab + Ya + Yb)}$$

Where x = the number of times a and b were observed together, either in contact or within 3 m of each other; Ya = only a was observed; Yb = only b was observed; Yab = a and b were observed separately (i.e., not in contact and more than 3 m apart).

Four networks were developed to explore differences in proximity and contact between individuals. Two were based on direct interactions (gorillas in physical contact), while the other two were based on proximity (gorillas within 3 m of each other). For direct comparison, each type of network (contact and proximity) was constructed for both the presence and absence of visitors. This approach allows us to quantify how interactions and proximity between individuals may be influenced by the presence of visitors, thereby highlighting their direct impact on social relationships within the studied troop. Additionally, to determine whether the presence of visitors affects the type of interactions observed between gorillas, the occurrence of the different interactions described above was compared using a paired t-test.

3.1.3. Eigenvector centrality

The network of interactions within the troop can be characterised by a centrality value, which indicates the number of direct connections an individual has with other group members, who themselves have connections with their own neighbours. An individual exhibits high centrality if they are well-connected and interact extensively with other individuals, who are also interconnected. This metric helps identify key individuals who play a crucial role in the social structure of the group. Conversely, individuals with low centrality are situated on the periphery of the network with minimal interactions. According to Létang et al. (2021), who studied the same gorilla troop, the two adult males and the castrated sub-adults (Djomo (Djo) and Mawete (Maw)) should occupy central positions and thus have high centrality values relative to other adults in the troop, due to their potential interactions with all age and sex classes. In contrast, given the age of the juveniles, their centrality should also be quite high, likely inversely proportional to their age.

Additionally, it is expected that females will interact significantly with each other. [Stoinski et al. \(2003\)](#) found that beyond six months post-partum, there are more female-female and female-young interactions compared to interactions with the silverback or other adult males. Consequently, older individuals and silverbacks are anticipated to be on the periphery of the network and thus have lower centrality values. At the troop level, if interactions increase in the presence of visitors, significant differences in the centrality of certain individuals within the network should emerge, potentially impacting the overall average centrality values.

We first conducted several paired Student's t-tests to assess potential differences in the average centrality values of individuals in the presence and absence of visitors within the proximity contact networks. Subsequently, we evaluated the evolution of centrality values for each individual across the two types of networks.

3.1.4. Personality traits

Individual differences in behaviour can significantly influence an animal's role within a social network or its spatial use in response to visitors. To avoid subjective or anecdotal interpretations of personality traits based solely on the observer's empirical experience, we quantified the primary character traits using the protocol established by [Gold and Maple \(1994\)](#). Four keepers, each with over a year of experience working with the study group, independently completed evaluation forms (see factors and their scores in the appendix), rating each personality trait on a scale from 1 (not representative or absent) to 5 (highly representative). These traits were then categorised into four main personality dimensions for analysis: extroversion, dominance, fearfulness, and understanding. For instance, we hypothesised that an extroverted individual would be more likely to occupy the proximal zone in the presence of visitors, whereas a fearful individual might avoid it. Similarly, we would expect a dominant individual, rather than one characterised as understanding, to be involved in more agonistic interactions.

3.2. Spatial distribution and enclosure use

3.2.1. Presence of individuals in the proximal and distal zones

To evaluate the impact of visitors on the gorillas' use of their enclosure, we analysed the presence and absence of individuals in exposed and non-exposed zones in relation to both environmental and visitor-related variables. Given that the enclosure is bordered on both sides by pathways accessible to visitors, we were able to monitor the movements of the gorillas according to whether the public was present on one or both sides of the enclosure. Initially, we aimed to model changes in the number of individuals present in Proximal Zones as a function of these environmental and visitor variables. We also considered the time of day, which, based on observations, appeared to be a key predictor of space usage. As previously mentioned, we anticipated that high temperatures, wind, and rainfall would negatively affect the presence of individuals in the more open, weather-exposed Proximal Zones, leading them to prefer the more sheltered Distal Zones, which are covered in vegetation. Moreover, we expected that at least one of the visitor-related variables would have a significant influence on the presence of individuals in these exposed areas, even when controlling for climatic conditions, favouring the Distal Zones where the gorillas could more easily retreat from visitor visibility. As count data for Proximal Zone 1 (nP1) exhibited overdispersion, we employed a regression model with a negative binomial distribution, using the sampling day as a random factor to account for repeated observations of the same group. This procedure was also applied to the counts of individuals in Proximal Zone 2 (nP2) and the Distal Zones (nDis).

3.2.2. Exposure tolerance index (ETI)

Tolerance is defined as the degree to which gorillas accept being exposed to the sight of visitors within each of the proximal zones. It is expected that an older individual will exhibit lower tolerance in these

zones due to years of experience with visitor exposure, in contrast to a younger individual, whose curiosity and sensitivity to audience effects would likely result in a higher tolerance. Similarly, a more introverted gorilla is anticipated to have lower tolerance for exposure than an extroverted one.

The level of exposure tolerance is measured using a scale, which corresponds to a relative ratio of observation frequencies, normalised as a function the total number of observations of a given individual per zone, thereby allowing comparison of this index between different members of the troop.

For Proximal Zone 1, individual tolerance is quantified as follows:

$$ETI1 = \frac{\left(\frac{(a+d)}{m1} \right)}{\left(\frac{(b+c)}{m1} \right)}$$

Where a = observations of the gorilla in Zone P1 with no visitors present, b = observations of the gorilla in Zone P1 with visitors present in both V1 and V2, c = observations of the gorilla in Zone P1 with visitors present only in V1, d = observations of the gorilla in Zone P1 with visitors present only in V2, and $m1$ = total number of observations of the gorilla in P1.

An ETI1 value greater than 1 may indicate low tolerance to visitor exposure in this zone. This would correspond to the gorilla being observed more frequently in Proximal Zone 1 when there are no visitors, or only visitors in Zone V2 (i.e., on the far side of the enclosure), compared to when there are visitors all around the enclosure or only in Zone V1 (nearby).

An ETI1 value of 0 suggests that visitor presence has no influence (or neutral) on the gorilla's frequency of observation in P1.

An ETI1 value less than 0 can be interpreted as high tolerance to visitor exposure in this zone. This corresponds to the gorilla being observed more frequently in Proximal Zone 1 when visitors are present all around the enclosure or nearby in Zone V1, as opposed to when no visitors are present or they are confined to Zone V2 (i.e. on the other side of the enclosure)

For Proximal Zone 2, the ETI is similarly calculated as follows:

$$ETI2 = \frac{\left(\frac{(e+h)}{m2} \right)}{\left(\frac{(f+g)}{m2} \right)}$$

Where e = observations of the gorilla in Zone P2 with no visitors present, f = observations of the gorilla in Zone P2 with visitors present in both V1 and V2, g = observations of the gorilla in Zone P2 with visitors present only in V2, h = observations of the gorilla in Zone P2 with visitors present only in V1, and $m2$ = total number of observations of the gorilla in P2.

3.2.3. Retreat index (RI)

In addition to understanding the extent to which individuals in proximal zones tolerate the presence of visitors nearby, it is important to determine in which specific zone (V1 or V2) the presence of the public induce a defined retreat into the distal zone. To achieve this, we calculate a relative ratio between observations in the distal zone with and without visitors. We then use a Wilcoxon signed-rank test to compare the mean indices obtained for each visitor configuration, assessing whether the presence of visitors in V1, V2, or both zones simultaneously significantly affects the likelihood of individuals retreating to the distal zone

The indices are calculated as follows:

$$RI(V1V2) = \frac{\left(\frac{i}{m3} \right)}{\left(\frac{j}{m3} \right)}$$

$$RI(V1) = \frac{\binom{i}{m3}}{\binom{k}{m3}}$$

$$RI(V2) = \frac{\binom{i}{m3}}{\binom{l}{m3}}$$

Where i = number of observations of the individual in the distal zone without any visitors, j = number of observations of the individual in the distal zone with visitors in both V1 and V2, k = number of observations of the individual in the distal zone with visitors in V1 only, l = number of observations of the individual in the distal zone with visitors in V2 only, and $m3$ = total number of observations of the individual in the distal zone.

An index (RI) equal to 1 would suggest that the presence or absence of visitors has no effect on the individual's presence in the distal zone.

An index (RI) of less than 1 indicates that the individual is more frequently present in the distal zone when visitors are present (here in V1, or V2, or both simultaneously) than when they are absent, implying a retreat to this zone.

Conversely, an index (RI) greater than 1 suggests that the individual is more often found in the distal zone when there are no visitors present, indicating no retreat into the distal zone when visitors are present in V1, V2, or both.

3.2.4. Spatial dispersion patterns

To determine whether spatial dispersion models could be generalised across different visitor presence configurations, we extracted the coordinates of individuals under four conditions: in the absence of visitors, with visitors present only in zone V1, with visitors only in zone V2, and finally with visitors in both V1 and V2 simultaneously. We analysed these data using Ripley's L function, as proposed by Besag (1977) via the Spatstat package in R. This function represents a standardised version of Ripley's K function, originally introduced by Ripley B. D. in 1976 (Ripley, 1976), and further refined a few months later (Ripley, 1977). Ripley's function evaluates point distribution within a given space, helping to identify dispersion patterns. The standardisation of this function enhances linearity, facilitating interpretation. A key advantage of this function is that it provides results based on the distance scale "r", allowing us to assess dispersion patterns at both broad and fine scales. Here, we used the enclosure boundaries as the window for the possible distribution area in the function.

The $L(r)$ function is estimated as follows:

$$L(r) = \sqrt{\frac{K(r)}{\pi}}$$

And $K(r)$ is estimated as:

$$K(r) = \frac{a}{n(n-1)} \sum_i \sum_j I(d_{ij} \leq r) e_{ij}$$

Where a denotes the area of the window defining the potential distribution area, n is the total number of points considered relative to the sum of ordered point pairs i and j , d_{ij} represents the distance between two points i and j , and $I(d_{ij} \leq r)$ is an indicator equal to 1 if the distance is less than or equal to r . The term e_{ij} is the edge correction weight.

Ripley's function is typically employed to compare observed spatial point distributions with a random distribution. If $L(r)$ exceeds the reference line ($L(r) > r$), this indicates spatial clustering at that scale. Conversely, if $L(r)$ falls below the reference line ($L(r) < r$), it suggests spatial dispersion. If $L(r)$ closely follows the reference line, the distribution of points is considered random or regular. To ensure the reliability of this interpretation, a 95 % confidence interval is defined using a Monte Carlo procedure. When the curves of interest fall outside this interval, we can confidently infer a significant deviation from random

distribution patterns. One of the potential adjustments to this function, the edge correction, proves highly useful for a more refined interpretation of the spatial dispersion of gorillas. This correction accounts for observations made at the periphery of the study window, comparing them with those closer to the centre. It thus helps to reveal whether the gorillas exhibit a tendency to use the edges of their enclosure (e.g., near the canal or inner boxes) or, conversely, to remain closer to the centre, under varying conditions of interest.

4. Results

4.1. Inter-individual distances models

The presence of visitors in zone V1 had a notable effect on the distance between the silverback (Ya) and the two castrated males (SBM). Visitor presence at the time of observation (V1T), particularly when visitors were moving (V1N), resulted in a slight reduction in this distance (Est -7.617e-04, $P = 0.025$, and Est -9.589e-04, $P = 0.0001$, respectively). Conversely, a higher number of stationary visitors in this zone (V1Max) slightly increased the distance (Est 9.417e-04, $P = 0.006$). The presence of visitors in zone V2 had a significant impact on the distance between females and their young (DFY). Visitor presence at the time of observation (V2T) decreased this distance (Est -3.232e-03, $P = 0.003$), whereas an increase in the maximum number of visitors (V2Max) slightly increased it (Est 2.460e-03, $P = 0.023$).

When considering the combined presence of visitors in both zones V1 and V2, there was no significant effect on the various categories of inter-individual distances, except for the presence of moving visitors in both zones simultaneously (V1N*V2N). This decreased the average distance between individuals (ADI) (Est -0.027735, $P = 0.018$) while increasing the distance between Yaoundé and the castrated males (SBM) (Est 9.338e-05, $P = 0.007$).

Environmental factors, such as wind, humidity, and temperature, also influenced inter-individual distances. In general, these factors reduced the average distance between individuals (ADI) (Est -0.197554, $P = 0.015$; Est -0.074413, $P = 0.016$; Est -0.640310, $P = 5.01e-06$). Specifically, increases in humidity extended the distance between males (SBM) (Est 2.893e-04, $P = 0.0001$), as did rises in temperature (Est 1.383e-03, $P = 5.78e-05$), which also widened the distances between adult females (DAF) (Est 2.303e-03, $P = 0.0001$).

Time of day was another factor influencing specific inter-individual distances. In the afternoon, distances between males (SBM) (Est 8.939e-03, $P = 2.41e-05$), females with other females and females with silverback (DAF and DSF) (Est 1.146e-02, $P = 0.003$; Est 1.034e-02, $P = 0.005$), and juveniles with females (DFY) (Est 2.541e-02, $P = 0.0002$) were slightly higher than in the morning. However, when considering the group as a whole, the average distance (ADI) was approximately 5.28 m lower in the afternoon compared to the morning (Est -5.280682, $P = 1.13e-12$).

4.2. Social network analysis (SNA)

Using a quantitative approach, we calculated the difference in the number of contacts between the presence and absence of visitors. Shapiro tests revealed that the data distribution deviated significantly from normality ($P = 1.562e-07$), even after excluding the Mah-Mah (Ma) - Basoko (Ba) interaction, which, as shown in Fig. 2, exhibits markedly more interactions than other dyads ($P = 0.003$). Since the conditions for non-parametric testing were met, we applied a Wilcoxon signed-rank test for paired data, which indicated a significant increase in contact frequency in the presence of visitors compared to their absence ($P = 9.199e-05$, and $P = 0.0001$ without the (Ma) - (Ba) interaction). Given that female-infant interactions visually appeared to dominate the dataset, a Mann-Whitney U test was conducted to compare the difference in contact frequency between visitor-present and visitor-absent conditions, specifically for these pairs of interest against all other possible pairings.

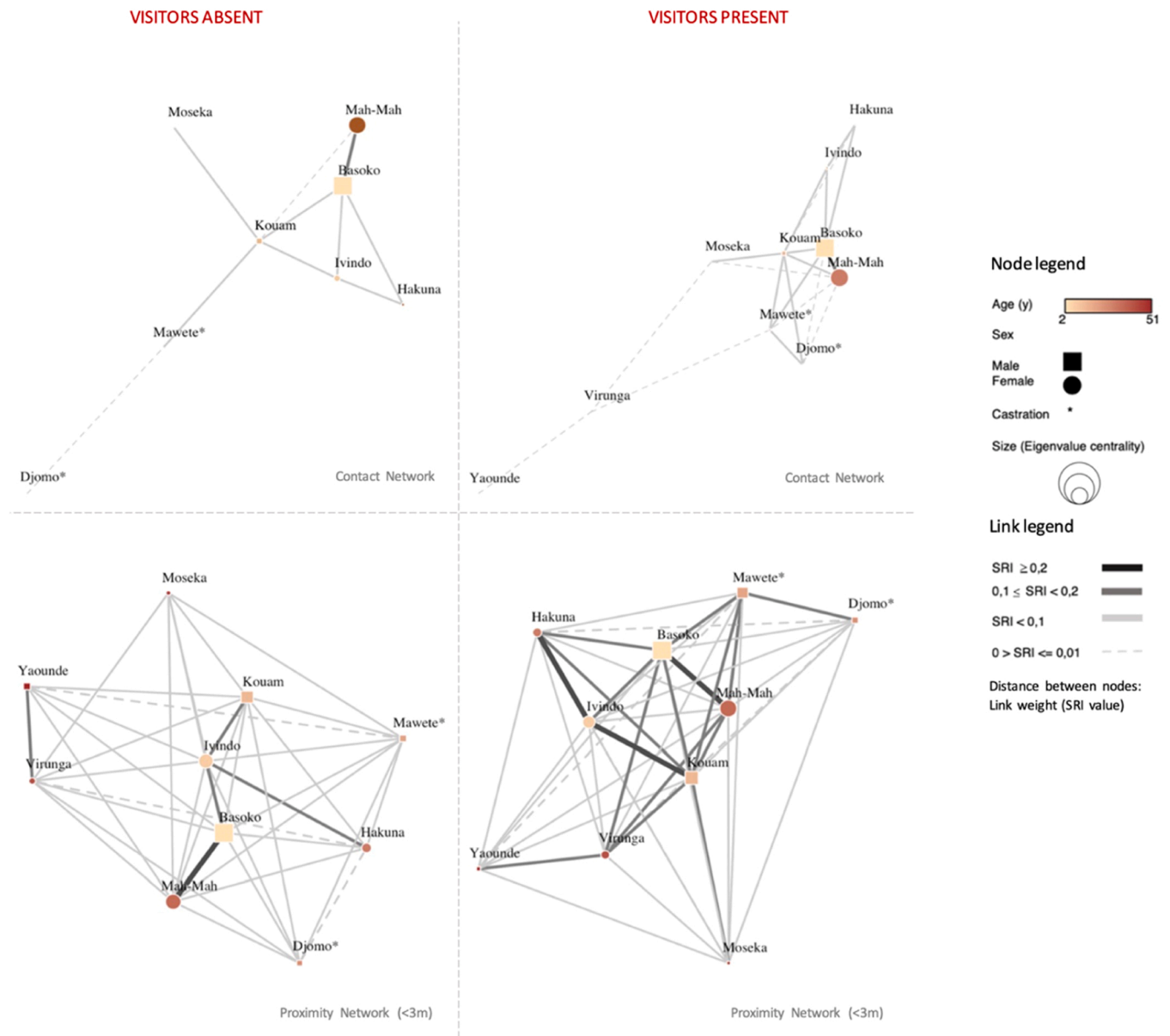


Fig. 2. Diagram of the 4 social networks for contact and interaction of the gorilla group housed at La Vallée des Singes (France). Yaoundé and Virunga were not involved in direct contacts without visitors during the study, so they are not represented on the corresponding network.

The results ($P = 0.042$) demonstrated a significantly higher increase in contact frequency in the presence of visitors for female-infant pairs compared to other pair types. The same analysis was performed to examine the differences in proximity events near points of direct contact. Again, the distribution was abnormal ($P = 9.73\text{e-}07$, and $P = 0.005$ without the (Ma) - (Ba) pair). The Wilcoxon signed-rank test similarly showed a significant increase in proximity between individuals in the presence of visitors ($P = 9.616\text{e-}09$, and $P = 1.422\text{e-}08$ without the (Ma) - (Ba) pair). Likewise, the Mann-Whitney U test revealed that proximity in the presence of visitors was significantly higher between females and their offspring compared to other pair types ($P = 0.026$).

4.3. Eigenvectors centrality

Average eigenvector centrality values remained consistent, regardless of the presence of visitors, both in contact networks (Student's T-test for paired data, $P = 0.499$) and proximity networks ($P = 0.675$). This indicates that, on average, individuals' roles within these networks were not significantly influenced by the presence of visitors. However, a

closer analysis reveals notable individual variations in centrality. Specifically, two juveniles, Kouam and Ivindo, experienced a decrease in centrality when visitors were present, as did Hakuna, an adult female. By contrast, the centrality of other individuals remained relatively stable. In the contact networks, individuals with the lowest centrality scores were Djomo, Mawete, and Moseka—the two castrated males and the second oldest female. These values did not change with the presence of visitors. Conversely, individuals with higher centrality values, such as Mah-mah and her infant, Basoko, retained their prominent roles, even in the presence of visitors. In the proximity networks, Mah-mah and Basoko consistently exhibited high centrality when visitors were present, whereas individuals like Yaoundé and Moseka showed lower centrality. Interestingly, intermediate centrality values fluctuated more in the presence of visitors, particularly for individuals like Virunga, Mawete, Kouam, Ivindo, and Mah-mah. Therefore, while average centrality values suggest overall stability, the variations between specific individuals reveal a more nuanced effect of visitor presence on network dynamics.

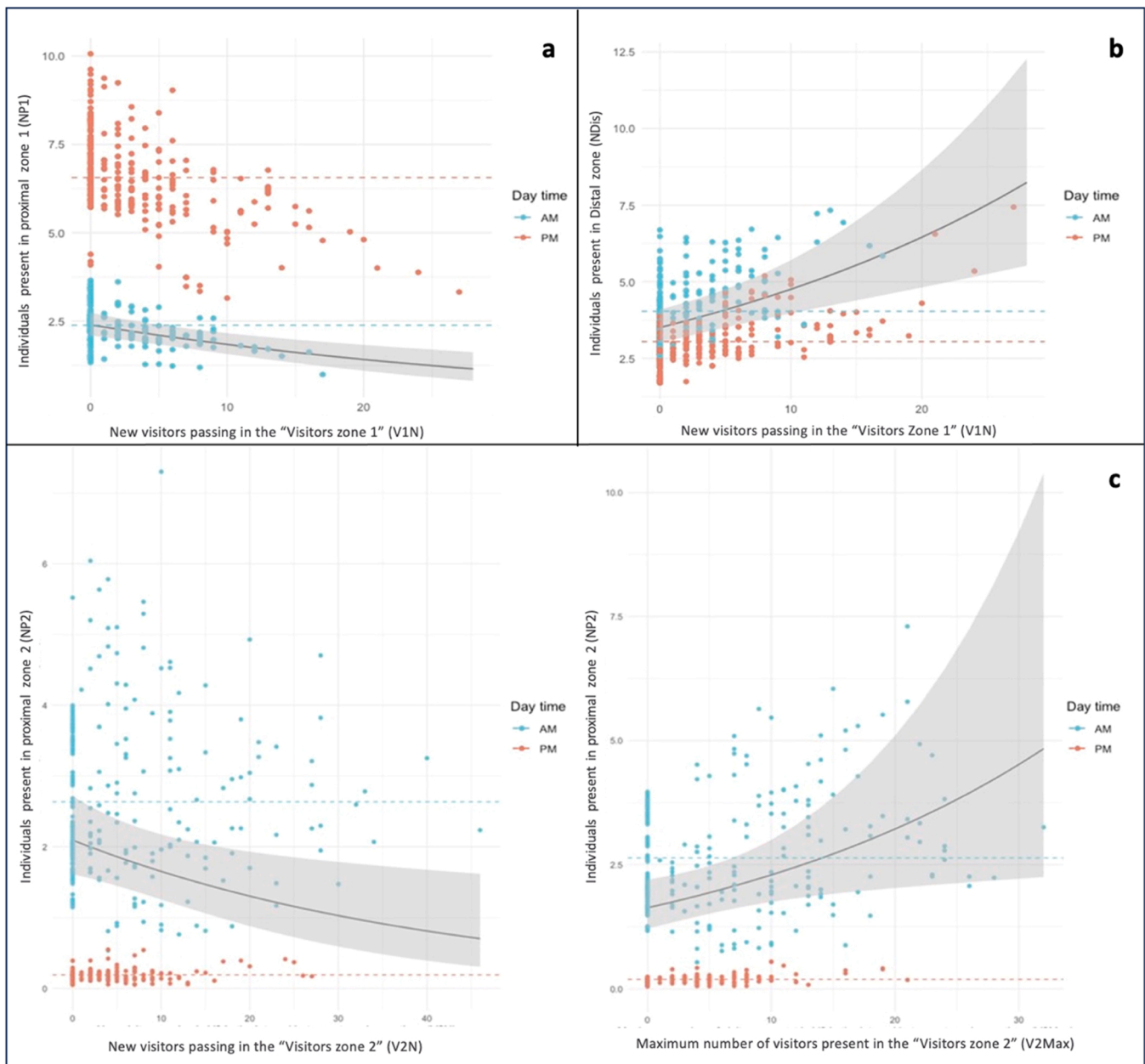


Fig. 3. Graphical representation illustrating the impact of new visitors passing through visitor zones 1 (V1N) and 2 (V2N), along with the maximum number of visitors in zone 2 (V2Max), on gorilla distribution across the three enclosure zones: Proximal 1 (NP1) in panel "a", Distal (NDis) in panel "b", and Proximal 2 (NP2) in panel "c".

4.4. Nature and occurrence of interactions

Regardless of the type of contact, the frequency of interactions was consistently higher when visitors were present compared to their absence. On average, 22.44 (± 19.8) more interactions were recorded in the presence of visitors. Moreover, the majority of these contacts involved comfort or play behaviours, such as playing, resting, and sleeping. Certain types of interactions, including the sharing of a wooden branch or manipulating the enclosure's barriers, were observed exclusively when visitors were present. Finally, agonistic behaviour (fighting) was observed only once, both in the presence and absence of visitors.

4.5. Presence in proximal and distal zones

Proximal Zone 1 (a)

The models revealed that the influx of new visitors passing through Visitor Zone 1 (V1N) was the most significant factor in reducing the number of gorillas present in Proximal Zone 1 (P1) (Est -0.0262284 , $P=4.92e-05$). In contrast, the mere presence of visitors (V1T) or a large audience in Visitor Zone 1 (V1Max) showed no significant impact ($P=0.727$ and $P=0.295$, respectively).

Distal Zone (b)

To model the number of gorillas in the Distal Zone, we incorporated interactions between different visitor-related variables to explore their combined effect. However, none of these interactions proved to be significant. The only significant factor was the presence of new, moving visitors in Visitor Zone 1 (V1N), which led to a notable increase in the number of individuals in the Distal Zone (Est $3.285e-02$, $P=0.0002$).

Proximal Zone 2 (c)

On the opposite side of the enclosure, two visitor-related variables were found to significantly influence the number of gorillas in Proximal

Zone 2. Similar to Proximal Zone 1, the movement of new visitors (V2N) reduced the number of gorillas in this area (Est -0.023711 , $P=0.013$), while a large audience (V2Max) slightly increased it (Est 0.033926 , $P=0.017$).

Environmental variables and time of day also played a role in gorilla distribution across zones. Wind reduced the number of gorillas in Proximal Zone 1 ($P=0.0003$) while increasing the number in the Distal Zone ($P=9.28e-05$). Humidity and temperature were both found to decrease the number of gorillas in Proximal Zone 1 ($P=0.0369$ and $P=0.035$, respectively), with temperature also significantly reducing the number in Proximal Zone 2 ($P=0.002$). There were also significantly more gorillas in Proximal Zones 1 and 2 in the afternoon than in the morning ($P=2e-16$ for both), and fewer gorillas in the Distal Zone during the afternoon compared to the morning ($P=0.011$).

4.6. Exposure tolerance index (ETI) and retreat index (RI)

This figure illustrates the Retreat Indexes (RI) triggered by visitors in Zone 1 (RIV1) and Zone 2 (RIV2) independently, as well as concurrently in both zones (RIV1V2). The second part presents a correlation matrix (using the `cor.mtest` function from the `corrplot` package in R), showing only the significant correlations between the two types of indices, as well as age, sex, and personality traits.

The results indicate a RIV1V2 value of less than 1, suggesting that the gorillas retreat more towards the distal zone when visitors are present in both visitor zones 1 and 2 simultaneously, compared to when visitors are absent. However, there is no clear retreat pattern when visitors are present only in zone 1 or zone 2. In these cases, index values RIV1 and RIV2 are greater than 1, signifying that gorillas are more likely to remain in the distal zone in the absence of visitors, compared to when the public is present in either zone 1 or zone 2 individually.

By comparing the values of the three retreat indices using Wilcoxon signed-rank tests, a significant difference was identified in the retreat behaviour of individuals when visitors occupied both zones (RIV1V2), compared to when visitors were present only in zone 1 (RIV1) ($P=0.002$) or only in zone 2 (RIV2) ($P=0.002$). However, no significant difference was found between the retreat behaviour in the distal zone when visitors were in zone 1 (RIV1) compared to zone 2 (RIV2) ($P=0.275$). When focusing on key personality traits (Fig. 4), it becomes apparent that younger individuals tend to be the least fearful and the most extroverted. In contrast, the most fearful individuals are also the

oldest and demonstrate the highest levels of understanding. An individual profile based on the calculated indices reveals that younger gorillas do not show a strong tendency to retreat to the distal zone when visitors are present in both visitor zones (V1 and V2), unlike older individuals. Moreover, extroversion appears to be a strong predictor of retreat behaviour, as individuals with a higher retreat index (RI) are also those that exhibit more extroverted traits. Additionally, females in the group scored higher on traits related to understanding and fear, were generally older, displayed more dominance-associated behaviours, and were more tolerant of exposure to visitors in both proximal zones than males. Males, by contrast, were less inclined to retreat to the distal zone in the presence of visitors (indicated by higher RI values) and exhibited greater extroversion than females.

Based on the calculated indices, gorillas that exhibited the least exposure in proximal zone 1 to visitors in adjacent visitor zone 1 (and thus had a high ETI1 value) were also the oldest and most introverted. Conversely, those in proximal zone 2 with the least exposure to visitors in visitor zone 2 (high ETI2 value) were the most dominant individuals. Finally, a negative correlation was found between high ETI values (indicating low tolerance to visitor exposure) and low retreat indices, suggesting that gorillas with the least exposure tolerance to visitors were also those least likely to retreat to the distal zone when visitors were present.

4.7. Spatial dispersion patterns

The spatial distribution of gorillas under the four possible visitor presence/absence configurations was analysed using Ripley's models (Fig. 5). The $L(r)$ value quantifies the number of events (here, gorilla observation points) within a distance "r" or less from a reference event, on average, compared to what would be expected from a random spatial distribution. For instance, in the absence of visitors (situation "a" in Fig. 5), at a radius of 5 units ($r=5$ m), there are approximately six times as many gorilla observations ($L(r)=6$) around each reference point as would be expected from a random distribution. In all cases, the curves representing the actual point distribution ($Liso(r)$) lie above the $Lpois(r)$ curve and outside the confidence interval, indicating a significant tendency towards aggregation across all tested configurations.

Situation "a", with no visitors present, serves as a control for comparison. A slight but significant tendency towards aggregation is observed, even when considering point-to-point distances. The

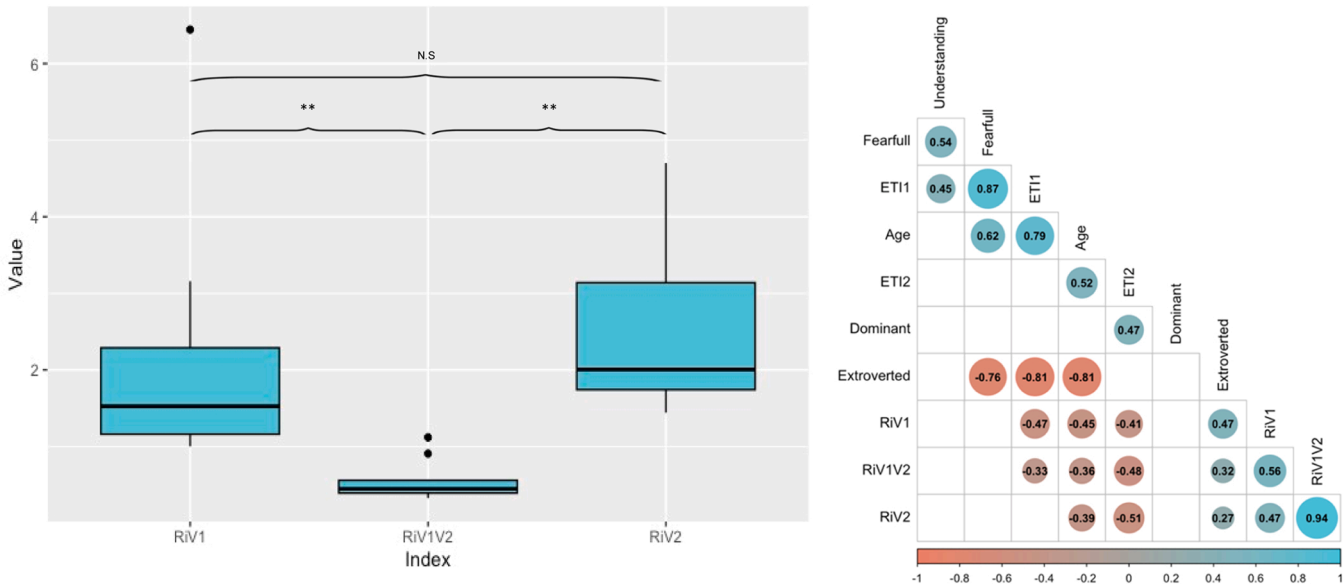


Fig. 4. Retreat (RI) and Tolerance (ETI) values and correlations. For clarity, only statistically significant correlations within a 95 % confidence interval are included in the correlation matrix.

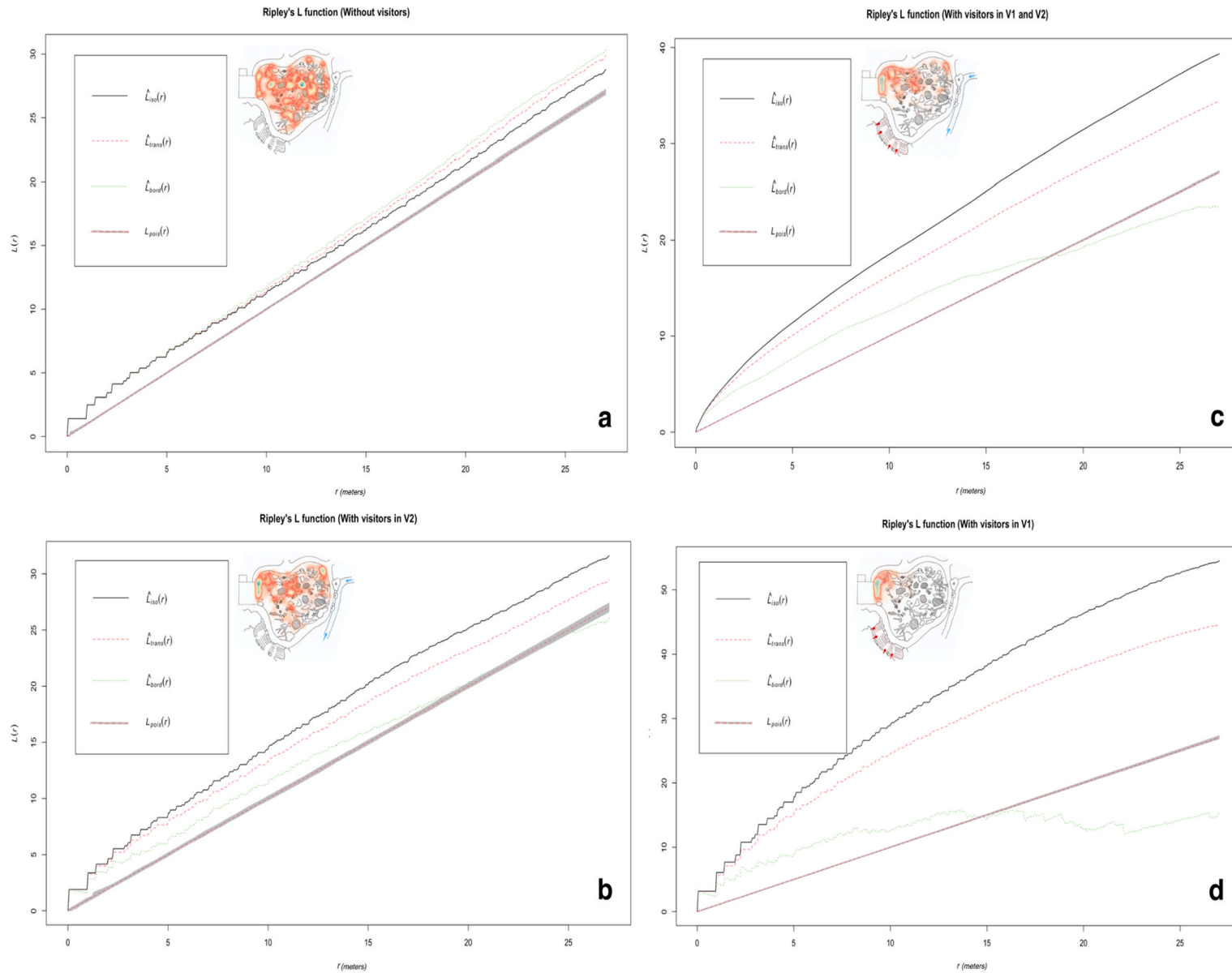


Fig. 5. Graphical representation of Ripley's L(r) functions in the absence and presence of public in visitor zone 1 (V1), 2 (V2) or both simultaneously. The solid black curve represents the observed spatial distribution, while the dotted red curve reflects a transformation where r is subtracted from the observed $L(r)$ function to account for the actual distances between observation points. The dotted green curve represents edge correction, adjusting for the contribution of observations at the periphery of the study area compared to those in the centre. The dotted red line, $L_{\text{pois}}(r)$, surrounded by grey shading, corresponds to the theoretical $L(r)$ function for a Poisson process, representing a random spatial distribution within the defined space. To aid interpretation, the confidence interval obtained through the Monte Carlo procedure is displayed in grey around the random dispersion model. These models were generated using the R Spatstat package, with the territory boundaries set as the maximum distribution window. Additionally, a small heat map is included for each scenario to visually depict the actual distribution of observation points within the enclosure.

contribution of points at the boundary is comparable to those in the centre, suggesting that the gorillas are relatively uniformly distributed across the entire area and this contribution increases linearly across different spatial scales. We define this as a quasi-random distribution, as there are no substantial deviations when compared to the other scenarios.

Situation "b" (with visitors present only in visitor zone 2) is similar to situation "a" in terms of linearity across spatial scales. However, in this case, the degree of aggregation is nearly double for all values of r . Beyond larger spatial scales ($r=20$), the contribution of points at the edges of the territory becomes insignificant, indicating a stronger concentration of gorilla sightings towards the centre of the enclosure. Early signs of clustering appear locally, and peripheral points are much less evenly distributed than in situation "a".

In situation "d" (with visitors present only in visitor zone 1), the degree of aggregation is even greater, with the clustering more focused towards the centre of the territory. Here, the contribution of points at the edges becomes insignificant at $r=15$, meaning that central points contribute more to the observed aggregation. This is reflected by the black and red curves being significantly higher than the random distribution, demonstrating a much stronger tendency towards aggregation compared to situations "a" and "b", across all spatial scales.

Finally, situation "c" (with visitors present in both visitor zones 1 and 2, i.e., surrounding the enclosure) represents an intermediate scenario. The tendency towards aggregation is stronger than in situation "a" but sits between situations "b" and "d". The contribution of points at the enclosure's boundary is locally significant, becoming negligible at around $r=18$, positioning it once again between the results of situations "b" and "d".

5. Discussion

Overall, while all environmental variables similarly influenced gorilla behaviour, the visitor-related factors examined in this study induced distinct changes in individual interactions and the distribution of gorillas within the enclosure. The mere presence of visitors (VnT) and large groups of visitors (VnMax) only sporadically affected distances between certain pairs of individuals, sometimes in opposite directions, without revealing a clear underlying behavioural pattern. In contrast, the flow of new visitors along the paths surrounding the enclosure (VnN) consistently impacted the spacing between all classes of individuals, reducing overall troop dispersion while prompting a shift towards the more sheltered distal zone. As anticipated, this zone served as a refuge from climatic variations, but visitor-related factors remained the strongest predictor of gorilla retreats to this zone when analysed within the same models. Other factors, such as rainfall, could not be assessed in this study due to the unusually dry conditions during the observation period. However, it is highly likely that rainfall would have encouraged greater use of the more wooded distal zone, providing better cover.

Regarding spatial dynamics, we focused on interactions involving Yaoundé, the silverback, and his two castrated sons, Djomo and Mawete. Castration is a relatively recent population management strategy for this species in captivity, and data on interactions involving castrated males within a troop are scarce. Our findings revealed that these two castrated males had the lowest eigenvector centrality scores in the group, reflecting their peripheral roles within the social network. Building on the observations of Létang et al. (2021), who studied these individuals six years prior, we observed cohesive individuals engaging in positive interactions with other troop members. However, these castrated males frequently occupied a social periphery, primarily interacting with each other (see Fig. 2), and their number of social interactions decreased when the group's spatial aggregation peaked. This likely reflects an avoidance strategy towards the silverback, as the distance between these two young males and the silverback was consistently the greatest across all distance classes.

Change to the sound environment caused by visitors, as discussed by

Hashmi and Sullivan (2020), is another potential disruptor that was not measured in this study. However, our results highlight the importance of disentangling the specific effects of visitor presence to implement practical welfare measures for captive animals. For example, our findings support the hypothesis that the visibility of visitors has a greater influence on gorilla behaviour than merely hearing them. Lewis et al. (2020), who directly measured visitor-induced noise disturbance, failed to isolate a significant effect independent of other visitor-related variables. Previous research has shown that simply hiding visitors from gorillas, regardless of their number or noise level, significantly reduces aggression and stereotypies (Blaney and Wells, 2004). Our results align with this, showing a stronger behavioural response to visitors in Zone 1 (V1) compared to Zone 2 (V2), with a marked retreat into the distal zone and increased spatial aggregation. As illustrated in Fig. 1, Zone 2 (V2) is covered by trees, making it harder for gorillas to see visitors, whereas Zone 1 (V1) is largely open, enabling clear visibility of all visitors present. Furthermore, Zone 1 is the site of public feeding sessions, likely contributing to higher disturbance levels or, at the very least, a consistent human presence.

Regardless of environmental factors, our results suggest that the distal zone serves as a refuge for gorillas seeking to avoid visitor-induced disturbances. The analysis of the Retreat Index (RI) and Exposure Tolerance Index (ETI) reveals that younger, more extroverted, and less fearful gorillas were more likely to remain near visitors (in proximal zones) during their presence, as reflected in higher RI values. Conversely, older, more introverted, and fearful individuals exhibited the opposite trend, with lower RI values. Although the RI and ETI provide valuable insights, caution is required when interpreting these results. While they offer an understanding of field observations, they do not fully capture the broader captive gorilla population due to strong individual differences influencing behavioural outcomes. The Exposure tolerance index measured in Proximal Zone 1 (ETI1) exemplifies this issue. According to the index, older, more introverted individuals were the most likely to remain in this zone, which might seem counterintuitive. However, this is largely due to the data from one female, Moseka, who is the second oldest and most introverted individual yet frequents proximal zone 1 regularly. Our observations suggest her presence in this zone is motivated by her solitary nature, as she tends to avoid other gorillas and seeks areas with fewer individuals, such as proximal zone 1, when visitors are present. This bias creates a negative correlation between the ETI and the RI, as shown in Fig. 4. These results indicate that even when gorillas show low tolerance for visitors, they do not always retreat to more distant zones, and social dynamics remain a significant factor in their spatial dispersion, underscoring the complexity of their behavioural responses to visitor pressure. The scope of these findings is further limited by the fact that this study involved only 10 gorillas from a single troop as a preliminary methodology test. Replicating this study with other captive gorilla groups will be essential for a more comprehensive interpretation of these indices.

Although tested on captive gorillas, these indices are designed for adaptation to various species and enclosures where animals encounter visitor-related disturbances. The retreat index (RI) and the exposure tolerance index (ETI) can be applied to any species exhibiting variability in spatial behaviour and tolerance to human presence. The complexity of the enclosure and the availability of hiding places from public view significantly influence individual behaviour, as previously observed in other primates. Similar behavioural responses to visitor stimuli have also been documented in other species, such as big cats (Sellinger and Ha, 2005), ungulates (Mansour et al., 2000, Shen-Jin et al., 2010), small mammals (Learmonth et al., 2018), and birds (Sherwen et al., 2015, Hoy and Brereton, 2022), all of which could benefit from these indices. Moreover, the versatility of these tools allows for their adaptation to different types of exhibits, ranging from open exhibits to more enclosed environments. To facilitate their application in various contexts, we have included an additional flowchart in the appendix that outlines the step-by-step process for data collection, index calculation, and

interpretation. The goal is to make this methodology accessible and practical for both researchers and zoo professionals, promoting the integration of these tools into animal welfare assessments, studies conducted in captivity, and enclosure design.

This study confirmed, through various approaches, that gorillas tend to aggregate in the presence of visitors, a behaviour supported by Ripley's models. Notably, this aggregation did not lead to increased agonistic behaviours; most individuals exhibited comfort or resting behaviours, with no signs of heightened aggression, stereotypes, or self-mutilation during the study period. These results, derived from Ripley's functions, also account for the tendency of individuals to remain close to their buildings, as observed by Ogden et al. (1993) and Ross and Lukas (2006), as well as the boundaries of their territory, using edge corrections. Even in the absence of visitors, a slight but significant tendency towards aggregation was observed. This is likely due to the habitat's non-uniform matrix, with certain paths between bushes and trees being more frequently used, resulting in a natural slight aggregation across all observations. One limitation of our methodology was the use of paper maps for tracking gorilla locations, which we strongly recommend replacing with devices incorporating ArcGIS, QGIS, or other GIS systems. These would enable faster, more accurate positioning, eliminate the need for digitising observation points, and make subsequent data analysis more efficient. The potential use of other techniques borrowed from statistical physics, such as the radial distribution function $G(r)$, which is used to describe the spatial distribution of particles and the probability of finding a particle at a specific distance from a reference particle (Stachurski, 2015; Wade et al., 2018), could be explored in the future. This concept should also apply to the spatial coordinates of animals, allowing the evaluation of spatial attraction or repulsion between observation points, akin to particle systems. Additionally, the bivariate version of this function could be utilised to examine finer interactions between different groups, such as males and females.

This study reiterates the importance of incorporating retreat zones in captive enclosures, echoing the recommendations of Hashmi and Sullivan (2020). These zones provide a protective buffer against visitor disturbances, giving animals the option to remain visible or retreat from view. This is particularly critical for more fearful, introverted, or older animals, which are more sensitive to such interactions. Research suggests that viewing animals in naturalistic enclosures improves perceptions of animal welfare, attraction, and educational value (Melfi et al., 2004; Nakamichi, 2007; Kutska, 2009). However, the impact of animal visibility on the overall zoo experience remains debated, with some studies suggesting that visitors spend more time near enclosures where animals are active and visible (Altman, 1998; Anderson et al., 2003; Godinez et al., 2013), while others argue that visitors' efforts to locate animals increase their engagement (Phillip, 1996).

6. Conclusion

Here we present a methodological framework for assessing the complex effects of visitors on the behaviour and spatial dynamics of captive gorillas, focusing on interactions between individual variability, environmental factors, and visitor dynamics. Our findings reveal that it is not merely the presence, activity or number of visitors that matters; gorillas adapt their spatial distribution based on their perception of visitors, while maintaining social cohesion in this case, without increasing agonistic interactions. The Retreat Index (RI) and Exposure Tolerance Index (ETI) provide valuable measures for assessing individual variability in gorilla responses to human-induced disturbances. These indices enhance our understanding of how different individuals cope with visitor presence, offering practical implications for enclosure design. However, further replication across different contexts is necessary to refine their application. The use of Ripley functions emerges as a sensitive and relevant tool for analysing spatial distribution in captivity. This approach allows for the identification of areas most frequented by

gorillas and facilitates testing of group dispersal across different scenarios. Our results suggest a strong aggregation of gorillas in the presence of visitors, with a notable shift towards the centre of the study zone, overlapping with the defined distal zone. This finding underscores the necessity for enclosures that incorporate retreat areas, particularly for individuals more sensitive to disturbances. Beyond its implications for gorilla management, this study underscores the importance of an integrative approach to accurately characterise the visitor effect. Future applications of this methodology should enable the refinement of management strategies for enclosures and areas accessible to the public, promoting the well-being of a wide variety of species in captivity and allowing animals greater control over their exposure to human presence.

Ethical Note

Our research was conducted in an observational and completely non-invasive manner with western lowland gorillas (*Gorilla gorilla gorilla*) in the outdoor enclosure of a zoological parc. No animals were harmed during the study, and the study involved no direct interaction, manipulation or interference with the gorillas, ensuring minimal disruption of their natural behavior. The observation protocol was reviewed in collaboration with the zoo's direction and the caretakers who look after the gorillas on a daily basis, to ensure that any observations made at a distance did not disturb the individuals. The research in this study did not require the control of any institutional or governmental regulatory body.

CRediT authorship contribution statement

Hugo Leroy: Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Software, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Jean-Pascal Guery:** Writing – review & editing, Validation, Resources, Project administration, Data curation. **Calogero Montedoro:** Writing – review & editing, Supervision, Methodology, Conceptualization. **Thierry Hance:** Writing – review & editing, Validation, Supervision, Resources, Project administration, Methodology, Formal analysis, Conceptualization.

Declaration of Generative AI and AI-assisted technologies in the writing process

During the preparation of this work, the authors used Grammarly and GPT-3.5 model for grammar correction. After using this tool/service, the authors reviewed and edited the content as needed and take full responsibility for the content of the publication.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

The authors thank the teams of caretakers and all the staff at la Vallée des Singes for their collaboration and sympathy throughout the data collection process. We would also like to thank the members of the Earth and Life Institute, Biodiversity Research Centre for the provision of data collection equipment and access to the in-house library. This paper is publication BRC 424 of the Biodiversity Research Center (Université catholique de Louvain, Belgium).

Appendix A. Supporting information

Supplementary data associated with this article can be found in the

online version at [doi:10.1016/j.applanim.2024.106433](https://doi.org/10.1016/j.applanim.2024.106433).

Data Availability

Data are available from the Mendeley Data repository: <https://doi.org/10.17632/4rd9g6cdf1>

References

- Altman, J.D., 1998. Animal Activity and Visitor Learning at the Zoo. *Anthrozoös* 11 (1), 12–21. <https://doi.org/10.1080/08927936.1998.11425083>.
- Anderson, U.S., Benne, M., Bloomsmith, M.A., Maple, T.L., 2002. Retreat space and human visitor density moderate undesirable behavior in petting zoo animals. *J. Appl. Anim. Welf. Sci.: JAAWS* 5 (2), 125–137. https://doi.org/10.1207/S15327604JAAWS0502_03.
- Anderson, U.S., Kelling, A.S., Pressley-Keough, R., Bloomsmith, M.A., Maple, T.L., 2003. Enhancing the Zoo Visitor's Experience by Public Animal Training and Oral Interpretation at an Otter Exhibit. *Environ. Behav.* 35 (6), 826–841. <https://doi.org/10.1177/0013916503254746>.
- Besag, J., 1977. Discussion on Dr Ripley's Paper. *J. R. Stat. Soc. Ser. B Methodol.* 39 (2), 192–212. <https://doi.org/10.1111/j.2517-6161.1977.tb01616.x>.
- Blaney, E.C., Wells, D.L., 2004. The influence of a camouflage net barrier on the behaviour, welfare and public perceptions of zoo-housed gorillas. *Anim. Welf.* 13 (2), 111–118. <https://doi.org/10.1017/S0962728600026841>.
- Cairo-Evans, A., Wierzal, N.K., Wark, J.D., Cronin, K.A., 2022. Do zoo-housed primates retreat from crowds? A simple study of five primate species. *Am. J. Primatol.* 84 (10), e23386. <https://doi.org/10.1002/ajp.23386>.
- Carr, N., 2016. An analysis of zoo visitors' favourite and least favourite animals. *Tour. Manag. Perspect.* 20, 70–76. <https://doi.org/10.1016/j.tmp.2016.07.006>.
- Carter, M., Webber, S., & Sherwen, S. (2015). Naturalism and ACI: Augmenting Zoo enclosures with digital technology. *Proceedings of the 12th International Conference on Advances in Computer Entertainment Technology*, 1–5. <https://doi.org/10.1145/2832932.2837011>.
- Chamove, A.S., Hosey, G.R., Schaezel, P., 1988. Visitors excite primates in zoos. *Zoo. Biol.* 7 (4), 359–369. <https://doi.org/10.1002/zoo.1430070407>.
- Clark, P.J., Evans, F.C., 1954. Distance to Nearest Neighbor as a Measure of Spatial Relationships in Populations. *Ecology* 35 (4), 445–453. <https://doi.org/10.2307/1931034>.
- Dale, M.R.T., Dixon, P., Fortin, M.-J., Legendre, P., Myers, D.E., Rosenberg, M.S., 2002. Conceptual and mathematical relationships among methods for spatial analysis. *Ecography* 25 (5), 558–577. <https://doi.org/10.1034/j.1600-0587.2002.250506.x>.
- de Freitas Alves, G., de Santana, D.G., 2022. Why do traditional dispersion indices used for analysis of spatial distribution of plants tend to become obsolete? *Popul. Ecol.* 64 (2), 80–92. <https://doi.org/10.1002/1438-390X.12105>.
- Flohic, G.L., Motsch, P., DeNys, H., Childs, S., Courage, A., King, T., 2015. Behavioural Ecology and Group Cohesion of Juvenile Western Lowland Gorillas (*Gorilla g. Gorilla*) during Rehabilitation in the Batéké Plateaux National Park, Gabon. *PLOS ONE* 10 (3), e0119609. <https://doi.org/10.1371/journal.pone.0119609>.
- Glatston, A.R., Geilvoet-Soeteman, E., Hora-Peck, E., Van Hooff, J., 1984. The influence of the zoo environment on social behavior of groups of cotton-topped tamarins, *Saguinus oedipus oedipus*. *Zoo. Biol.* 3 (3), 241–253. <https://doi.org/10.1002/zoo.1430030307>.
- Godinez, A.M., Fernandez, E.J., Morrissey, K., 2013. Visitor Behaviors and Perceptions of Jaguar Activities. *Anthrozoös* 26 (4), 613–619. <https://doi.org/10.2752/175303713X13795775535850>.
- Gold, K.C., Maple, T.L., 1994. Personality assessment in the gorilla and its utility as a management tool. *Zoo. Biol.* 13 (5), 509–522. <https://doi.org/10.1002/zoo.1430130513>.
- Goodenough, A.E., McDonald, K., Moody, K., Wheeler, C., 2019. Are “visitor effects” overestimated? Behaviour in captive lemurs is mainly driven by co-variation with time and weather. *Article 2. J. Zoo. Aquar. Res.* 7 (2). <https://doi.org/10.19227/jzar.v7i2.343>.
- Hashmi, A., Sullivan, M., 2020. The visitor effect in zoo-housed apes: The variable effect on behaviour of visitor number and noise. *Article 4. J. Zoo. Aquar. Res.* 8 (4). <https://doi.org/10.19227/jzar.v8i4.523>.
- Hosey, G.R., 2005. How does the zoo environment affect the behaviour of captive primates? *Appl. Anim. Behav. Sci.* 90 (2), 107–129. <https://doi.org/10.1016/j.applanim.2004.08.015>.
- Hosey, G.R., Druck, P.L., 1987. The influence of zoo visitors on the behaviour of captive primates. *Appl. Anim. Behav. Sci.* 18 (1), 19–29. [https://doi.org/10.1016/0168-1591\(87\)90251-6](https://doi.org/10.1016/0168-1591(87)90251-6).
- Hoy, R.A., Brereton, J.E., 2022. Does Observer Presence Modify the Behavior and Enclosure Use of Captive Edwards' Pheasants? *Article 2. J. Zool. Bot. Gard.* 3 (2). <https://doi.org/10.3390/jzbg3020012>.
- Kint, V., van Meirvenne, M., Nachtergale, L., Geudens, G., Lust, N., 2003. Méthodes spatiales pour quantifier le développement de la structure des peuplements forestiers : A Comparison Between Nearest-Neighbor Indices and Variogram Analysis. *For. Sci.* 49 (1), 36. <https://doi.org/10.1093/forestscience/49.1.36>.
- Kiskowski, M.A., Hancock, J.F., Kenworthy, A.K., 2009. On the Use of Ripley's K-Function and Its Derivatives to Analyze Domain Size. *Biophys. J.* 97 (4), 1095–1103. <https://doi.org/10.1016/j.bpj.2009.05.039>.
- Kutska, D., 2009. Variation in visitor perceptions of a polar bear enclosure based on the presence of natural vs. Un-natural enrichment items. *Zoo. Biol.* 28 (4), 292–306. <https://doi.org/10.1002/zoo.20226>.
- Law, R., Illian, J., Burslem, D.F.R.P., Gratz, G., Gunatilleke, C.V.S., Gunatilleke, I. A. U. N., 2009. Ecological information from spatial patterns of plants: Insights from point process theory. *J. Ecol.* 97 (4), 616–628. <https://doi.org/10.1111/j.1365-2745.2009.01510.x>.
- Learmonth, M.J., Sherwen, S., Hemsworth, P.H., 2018. The effects of zoo visitors on Quokka (*Setonix brachyurus*) avoidance behavior in a walk-through exhibit. *Zoo. Biol.* 37 (4), 223–228. <https://doi.org/10.1002/zoo.21433>.
- Létang, B., Mulot, B., Alerte, V., Bionda, T., Britton, L., ter Meulen, T., Szánthó, J., Guéry, J.-P., Sueur, C., 2021. Social proximities of developing gorilla males (*Gorilla gorilla gorilla*) in European zoos: The consequences of castration and social composition. *Appl. Anim. Behav. Sci.* 234, 105175. <https://doi.org/10.1016/j.applanim.2020.105175>.
- Létang, B., Mulot, B., Alerte, V., Bionda, T., Britton, L., ter Meulen, T., Szánthó, J., Guéry, J.-P., Sueur, C., 2021. Social proximities of developing gorilla males (*Gorilla gorilla gorilla*) in European zoos: The consequences of castration and social composition. *Appl. Anim. Behav. Sci.* 234, 105175. <https://doi.org/10.1016/j.applanim.2020.105175>.
- Lewis, R.N., Chang, Y.-M., Ferguson, A., Lee, T., Clifford, L., Abeyesinghe, S.M., 2020. The effect of visitors on the behavior of zoo-housed western lowland gorillas (*Gorilla gorilla gorilla*). *Zoo. Biol.* 39 (5), 283–296. <https://doi.org/10.1002/zoo.21552>.
- Lynch, H.J., Moorcroft, P.R., 2008. A spatiotemporal Ripley's K-function to analyze interactions between spruce budworm and fire in British Columbia, Canada. *Can. J. For. Res.* 38 (12), 3112–3119. <https://doi.org/10.1139/X08-143>.
- Mansour, A.A.H., Zakaria, A.H., Fraser, A.F., 2000. Effect of Enclosure Quality on Reactivity and Welfare of Captive Soemmerring's Gazelle (*Gazella soemmerringii*). *J. Appl. Anim. Welf. Sci.* 3 (4), 335–343. https://doi.org/10.1207/S15327604JAAWS0304_5.
- Maple, T.L., Finlay, T.W., 1989. Applied primatology in the modern zoo. *Zoo. Biol.* 8 (S1), 101–116. <https://doi.org/10.1002/zoo.1430080511>.
- Melfi, V.A., McCormick, W., Gibbs, A., 2004. A preliminary assessment of how zoo visitors evaluate animal welfare according to enclosure style and the expression of behavior. *Anthrozoös* 17 (2), 98–108. <https://doi.org/10.2752/089279304786991792>.
- Moss, A., Esson, M., 2010. Visitor interest in zoo animals and the implications for collection planning and zoo education programmes. *Zoo. Biol.* 29 (6), 715–731. <https://doi.org/10.1002/zoo.20316>.
- Nakamichi, M., 2007. Assessing the Effects of New Primate Exhibits on Zoo Visitors' Attitudes and Perceptions by Using Three Different Assessment Methods. *Anthrozoös* 20 (2), 155–165. <https://doi.org/10.2752/175303707X207945>.
- Ogden, J.J., Lindburg, D.G., Maple, T.L., 1993. Preference for structural environmental features in captive lowland gorillas (*Gorilla gorilla gorilla*). *Zoo. Biol.* 12 (4), 381–395. <https://doi.org/10.1002/zoo.1430120408>.
- Parnell, R.J., 2002. Group size and structure in western lowland gorillas (*Gorilla gorilla gorilla*) at Mbeli Bai, Republic of Congo. *Am. J. Primatol.* 56 (4), 193–206. <https://doi.org/10.1002/ajp.1074>.
- Phillip, P. (1996). Visitor viewing behaviour in the Gaherty Reptile Breeding Centre, Jersey Wildlife Preservation Trust: A preliminary study. *Dodo*. (<https://www.semanticscholar.org/paper/Visitor-viewing-behaviour-in-the-Gaherty-Reptile-a-Philipp/99fa10586163af3fc4fac453b67bb0fa2f74f5>).
- Quick, D.L.F., 1984. An integrative approach to environmental engineering in zoos. *Zoo. Biol.* 3 (1), 65–77. <https://doi.org/10.1002/zoo.1430030107>.
- Ripley, B.D., 1976. The second-order analysis of stationary point processes. *J. Appl. Probab.* 13 (2), 255–266. <https://doi.org/10.2307/3212829>.
- Ripley, B.D., 1977. Modelling Spatial Patterns. *J. R. Stat. Soc. Ser. B (Methodol.* 39 (2), 172–192. <https://doi.org/10.1111/j.2517-6161.1977.tb01615.x>.
- Rose, P.E., Croft, D.P., 2015. The potential of Social Network Analysis as a tool for the management of zoo animals. *Anim. Welf.* 24 (2), 123–138. <https://doi.org/10.7120/09627286.24.2.123>.
- Rose, P.E., Scales, J.S., Brereton, J.E., 2020. Why the “Visitor Effect” Is Complicated. Unraveling Individual Animal, Visitor Number, and Climatic Influences on Behavior, Space Use and Interactions With Keepers—A Case Study on Captive Hornbills. *Front. Vet. Sci.* 7. (<https://www.frontiersin.org/articles/10.3389/fvets.2020.00236>).
- Ross, S.R., Lukas, K.E., 2006. Use of space in a non-naturalistic environment by chimpanzees (*Pan troglodytes*) and lowland gorillas (*Gorilla gorilla gorilla*). *Appl. Anim. Behav. Sci.* 96 (1), 143–152. <https://doi.org/10.1016/j.applanim.2005.06.005>.
- Sellinger, R.L., Ha, J.C., 2005. The Effects of Visitor Density and Intensity on the Behavior of Two Captive Jaguars (*Panthera onca*). *J. Appl. Anim. Welf. Sci.* 8 (4), 233–244. https://doi.org/10.1207/s15327604jaws0804_1.
- Shen-Jin, L., Todd, P., Yan, Y., Lin, Y., Hongmei, F., Wan-Hong, W., 2010. The effects of visitor density on sika deer (*Cervus nippon*) behaviour in Zhu-Yu-Wan Park, China. *Anim. Welf.* 19 (1), 61–65. <https://doi.org/10.1017/S0962728600001172>.
- Sherwen, S.L., Magrath, M.J.L., Butler, K.L., Hemsworth, P.H., 2015. Little penguins, *Eudyptula minor*, show increased avoidance, aggression and vigilance in response to zoo visitors. *Appl. Anim. Behav. Sci.* 168, 71–76. <https://doi.org/10.1016/j.applanim.2015.04.007>.
- Stachurski, Z.H., 2015. Fundamentals of amorphous solids: Structure and properties. Higher Education Press.
- Stoinski, T. s, Hoff, M. p, Maple, T. l, 2003. Proximity patterns of female western lowland gorillas (*Gorilla gorilla gorilla*) during the six months after parturition. *Am. J. Primatol.* 61 (2), 61–72. <https://doi.org/10.1002/ajp.10110>.
- Szmyt, J., 2014. Spatial statistics in ecological analysis: From indices to functions. *Silva Fenn.* 48 (1). (<https://www.silvafennica.fi/article/1008>).

- Torres, C.M., Poveda, M.T.A., Teijeiro, J.D.R., 2022. Morphological appearance and effects of castration on blackback gorillas *Gorilla gorilla gorilla* in the EAZA ex-situ population. Article 1. *J. Zoo. Aquar. Res.* 10 (1). <https://doi.org/10.19227/jzar.v10i1.616>.
- Turner, R., 2009. Point patterns of forest fire locations. *Environ. Ecol. Stat.* 16 (2), 197–223. <https://doi.org/10.1007/s10651-007-0085-1>.
- Vermeer, J., Abelló, M.T., Holtkötter, M., 2014. Progress in the Western lowland gorilla *Gorilla gorilla* European Endangered Species Programme: A review of the decade 2002–2011. *Int. Zoo. Yearb.* 48 (1), 234–249. <https://doi.org/10.1111/izy.12027>.
- Wade, A.D., Wang, L.-P., Huggins, D.J., 2018. Assimilating Radial Distribution Functions To Build Water Models with Improved Structural Properties. *J. Chem. Inf. Model.* 58 (9), 1766–1778. <https://doi.org/10.1021/acs.jcim.8b00166>.
- Wells, D.L., 2005. A note on the influence of visitors on the behaviour and welfare of zoo-housed gorillas. *Appl. Anim. Behav. Sci.* 93 (1), 13–17. <https://doi.org/10.1016/j.applanim.2005.06.019>.
- Williams, E., Carter, A., Rendle, J., Fontani, S., Walsh, N.D., Armstrong, S., Hickman, S., Vaglio, S., Ward, S.J., 2022. The Impact of COVID-19 Zoo Closures on Behavioural and Physiological Parameters of Welfare in Primates. Article 13. *Animals* 12 (13). <https://doi.org/10.3390/ani12131622>.
- Yamagiwa, J., Kahekwa, J., Basabose, A.K., 2003. Intra-specific variation in social organization of gorillas: Implications for their social evolution. *Primates* 44 (4), 359–369. <https://doi.org/10.1007/s10329-003-0049-5>.