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Public influence on social structure and habitat uses in captive western lowland gorillas (*Gorilla gorilla gorilla*) in a naturalistic enclosure



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*Mémoire présenté en vue de l'obtention du diplôme de
Master en Biologie des Organismes et Écologie.*

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Année académique 2022-2023

Pour l'entraînement à la synthèse d'informations et le respect de guidelines de revues, ce mémoire a été rédigé en suivant les Submission guidelines de la revue Behavioral Ecology and Sociobiology. Une exception cependant a été faite pour le nombre de page, pour permettre le développement d'un état de l'art pertinent et correspondant aux attentes d'un mémoire de fin d'étude. De même, la section Abstract et Significance statement ont été remplacés par un Abstract un peu plus complet suivi d'un résumé en français.

Public influence on social structure and habitat uses in captive western lowland gorillas (*Gorilla gorilla gorilla*) in a naturalistic enclosure

Hugo Leroy¹ 

Submitted: 14 August 2023 / supervised by Pr. T.Hance / C. Montedoro

Abstract

The present study analyzes how the presence of visitors affects the interactions and habitat use of a group of western lowland gorillas (*Gorilla gorilla gorilla*) living in a naturalistic enclosure. By relating the position of individuals, with an exposed/unexposed zone approach, to different visitor variables (density; movement or activity) acquired along two adjacent paths, we assessed how different situations of visitor presence influence gorilla behaviors. Our results suggest that visitors generally reduced inter-individual distances, accentuated by environmental factors such as wind, temperature, and humidity. Social network analysis revealed an intensification of contact, particularly between females and their offspring, as well as an increase in comfort and resting behaviors in the presence of visitors. Rather than large, immobile crowds, the presence of new visitors moving into the most exposed zone induced more retreat into the Distal (unexposed) zone, in contrast to the second possible zone, where visitors are harder for the gorillas to see. Overall, the different scenarios for the presence of visitors led to significant aggregation, contrasting with a quasi-random distribution without visitors. A new contribution is the introduction of the Retreat Index (RI), which indicates an individual's tendency to retreat into the unexposed zone, and the Exposure Tolerance Index (ETI), which quantifies individuals' tolerance of exposure to the sight of visitors. We also used Ripley's K and L functions, for the first time directly on individuals, revealing various spatial distribution patterns under different visitor configurations. This pilot study establishes a comprehensive protocol for analyzing the effects of visitors on captive gorillas, applicable to most housing conditions, which will need to be replicated to mitigate inter-individual variation and provide a global view of captive populations. Our methodological innovations shed light on the complex interaction between visitor presence, gorilla behavior and space use, and provide a basis for future investigations that will improve our understanding of the factors affecting gorilla dynamics in captivity.

Résumé

La présente étude analyse comment la présence de visiteurs affecte les interactions et l'utilisation de l'habitat d'un groupe de gorilles des plaines de l'Ouest (*Gorilla gorilla gorilla*), vivant dans un enclos semi-naturel. En reliant la position des individus, avec une approche de zone exposée/non exposée, à différentes variables de visiteurs (densité, mouvement ou activité) acquises le long de deux chemins adjacents, nous avons évalué comment différentes situations de présence de visiteurs influencent les comportements des gorilles. Nos résultats suggèrent que l'« effet visiteur » réduit globalement les distances interindividuelles, et est accentué par des facteurs environnementaux tels que le vent, la température et l'humidité. L'analyse des réseaux sociaux a révélé une intensification des contacts, en particulier entre les femelles et leur petits, ainsi qu'une augmentation des comportements de confort et de repos en présence de visiteurs. Plutôt que de grandes foules immobiles, la présence de nouveaux visiteurs se déplaçant dans la zone la plus exposée (V1) a induit plus de retrait dans la zone Distale (non exposée), contrairement à la deuxième zone possible (V2), où les visiteurs sont plus difficiles à voir pour les gorilles. Dans l'ensemble, les différents scénarios de présence de visiteurs ont conduit à une agrégation significative, contrastant avec une distribution quasi-aléatoire en l'absence de visiteurs. Une nouvelle contribution est l'introduction de l'indice de retrait (RI), qui indique la tendance d'un individu à se retirer dans la zone non exposée, et l'indice de tolérance à l'exposition (ETI), qui quantifie la tolérance des individus à l'exposition à la vue des visiteurs. Nous avons également utilisé les fonctions K et L de Ripley, pour la première fois directement sur des individus, révélant divers modèles de distribution spatiale sous différentes configurations de visiteurs. Cette étude pilote établit un protocole complet d'analyse des effets des visiteurs sur les gorilles captifs, applicable à la plupart des conditions d'hébergement, qui devra être reproduit pour atténuer les variations interindividuelles et fournir une vue d'ensemble des populations captives. Nos innovations méthodologiques mettent en lumière l'interaction complexe entre la présence de visiteurs, le comportement des gorilles et l'utilisation de l'espace, et fournissent une base pour de futures investigations, qui amélioreront notre compréhension des facteurs affectant la dynamique des gorilles en captivité.

Keywords Gorilla – Visitor effect – naturalistic enclosure – Ripley – social network analysis – Spatial distribution

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Introduction

Over the last few decades, there have been profound changes in the housing conditions for most animal species in captivity, including primates. Zoos have been given a role in educating and communicating with the public, and the presentation of animals in narrow, wire-fenced enclosures, devoid of any natural appearance, no longer really meets visitors' expectations (nor animal welfare conditions). In fact, the current standard for many zoos is to enlarge these enclosure and, for the third generation of 'zoo enclosure design', to mimic the animals' natural environment as closely as possible (Carter *et al.* 2015).

These enclosures, more conducive to the expression of natural behavior (Forthman Quick 1984, Mapple & Finlay 1989), rapidly became popular, increasing the quality of the 'Zoo Experience' (Hosey 2005) and the feeling of immersion. These changes in housing conditions necessarily led to significant differences in the behavior of encaged individuals. These have been described as increasing affiliative behavior, reducing stereotypy and agonistic interactions (Clarke *et al.*, 1982, Huffman *et al.* 2021). However, our current knowledge of the use of space and intra-group interactions within 'naturalistic' primate enclosures is still limited (Hosey 2005), and western lowland gorillas (*Gorilla gorilla gorilla*) are a highly relevant study model for learning more about this subject because their predominant use of land, even in non-natural environments (Ogden *et al.* 1993, Ross & Lukas 2006), makes a potential visitor effect on habitat use more easily observable.

This sub-species is the only one present in zoos (with the exception of an individual Eastern gorilla (*Gorilla beringei graueri*) at Antwerp Zoo) since the early 1950s. It is estimated that there are 750 western lowland gorillas in captivity worldwide, compared with 600 gorillas at the end of the 1990s, 43% of these were born in captivity (Mace 1988). The number of wild individuals is estimated at just over 360,000 (Strindberg *et al.* 2018). One of the major challenges, specific to captivity, is to try to maintain a demographically stable population over the long term while maintaining a sufficiently diverse gene pool. Although the assessment of juvenile survival rates suggested a gradual decline in heterozygosity in the captive population as a whole, it seems that compared with wild populations, western lowland gorillas (in North America at least) have significantly higher levels of allelic diversity and heterozygosity (Simons *et al.* 2013).

Some gorillas in captivity are maintained in small groups of males of 3 to 4 individuals, whose stability and risk of conflict depend in part on the age of the individuals at the time of contact (Stoinski *et al.* 2004). The other groups comprising females are organized in the same way as wild gorilla groups, i.e. polygynous social groups with an average of 8 to 10 individuals (Parnell 2002, Mittermeier *et al.* 2013). These are family groups, based around a single dominant silverback, as well as females, their juveniles, and sub-adult males (sometimes castrated to avoid over-representation of the genetic heritage of certain individuals in accordance with European breeding programs (EEP)). It is this second social group configuration that was followed for this study (see **Table 1**).

Several factors specific to the ecology of this species in captivity appear to affect interactions between individuals and the social structure as a whole. For example, castrated subordinate males (as opposed to 'intact' ones) are physically closer and interact more positively with other individuals in the group, of all sexes and ages (Létang *et al.* 2020). Le Flohic *et al.* (2015)

found that the degree of interactions in juvenile gorillas is linked to the nutritional quality of their diet, with their activity level and the occurrence of play behaviors correlated with their energy level. This suggests that a high-quality and varied diet plays a key role in the genesis of interactions between individuals, as well as reducing the occurrence of coprophagia and regurgitation/re-ingestion behaviors (Akers *et al.* 1985). Finally, parturition also seems to play a role in the way the social network is organised. In fact, in the first post-partum months, females interact more with other females and juveniles than with silverbacks (which runs counter to observations in *G. beringei*), and is therefore consistent with the theory that there is no risk of infanticide in captivity (Stoinski *et al.* 2003).

Western lowland gorillas, like chimpanzees or orangutans for example, are large mammals and, given their status as emblematic species, are of particular interest to the public (Moss & Esson 2010, Carr 2016). In captivity, this is reflected in the large numbers of visitors who gather around their territories to observe them. Previous studies have investigated the effect of visitors on captive primates, in relation to the presence or absence of visitors (Chamove *et al.* 1988, Williams *et al.* 2022), their density (see Thompson 1976, Glatston *et al.* 1984), or their activity (Hosey *et al.* 1987), and the physiological or behavioral responses induced by the presence of visitors have previously been described as having a negative, neutral, or sometimes positive effect. Wells (2005) described, for example, that a low visitor density would be conducive to more relaxation behavior and a significantly greater proportion of time spent resting and nesting. In contrast, a high visitor density would encourage intra-group aggression, stereotyped behavior, and self-mutilation. Most of these results were also observed by Williams *et al.* (2022) in a recent study that was studying the behavior of 4 primate species during the closure of zoos during the COVID-19 pandemic.

These behavioral anomalies in gorillas thus directly affect the interaction networks between individuals and their general well-being. However, they can be made less frequent and/or intense (see Carrasco *et al.* 2009) through positive re-injection training (PRT), interaction through play, regular cognitive stimulation (Clark 2011) or the provision of enrichment structures in the environment (Rooney *et al.* 1998).

It seems today that the quality of the environment takes precedence over the quantity of space available, particularly the presence of structural enrichments or the proximity of inner boxes (Ogden *et al.* 1993, Ross & Lukas 2006).

Finally, although it may seem obvious, certain environmental factors such as precipitation or temperature significantly affect the spatial distribution of individuals (Stoinski *et al.* 2001), making it more complex to study the visitor effect independently of these parameters.

Rose *et al.* (2020) demonstrated that for Black-helmeted Hornbills (*Ceratogymna atrata*), temperature could even be a better predictor of enclosure use than the presence of visitors.

There is currently no clear consensus on the visitor effect in primates, given the complexity of replicating experimental protocols in each site and the fact that individual variations in response to disturbance can be significant. Furthermore, all these studies done were carried out under different housing conditions, leading to just as many possible configurations of the visitor effect. This can have a considerable impact on the results obtained, especially as we know that the perception that animals have of visitors, whether it be the height from which they are observed (Chamove *et al.* 1988), the possibility of direct visual contact (Blaney *et al.* 2004) or the possibility of moving away from visitors (Cairo-Evans *et al.* 2022), directly affects the way in which they behave.

It seems that the methodologies used today have difficulty in specifically identifying the visitor effect on primate behavior. Lewis *et al.* (2020) compared the commonly used method of 'daily zoo-entry numbers (VGATE)' and the 'instantaneous crowds at the exhibit (VDENSITY)' and found that using new variables such as the direct density of visitors present (here *VDENSITY*) was a better predictor of individual behavior than the more commonly used (VGATE). Above all, this highlights the need to develop new methods for describing this disturbance and its effect on captive primates.

The aim of this study is to gain a better understanding of how gorillas perceive visitors in a naturalistic environment, and how this will affect their interactions and/or the way they exploit their territory. To do this, we are using innovative methodologies to compensate for current knowledge. We are using visitor-specific variables acquired by video-identification to disentangle those that

actually have an effect by relating them directly to the spatial distribution of individuals and their interactions. We are also using an exposed/unexposed zone approach to delimit the territory, enabling us to model territory use directly and to quantify for the first-time elements such as tolerance of exposure to visitors for each individual. We will also explore at the individual level the elements directly affecting behavioral response to the presence of visitors, using methods such as Ripley's K and L functions. This methodology, used for the first time directly for individuals, should enable us to accurately determine the aggregation or dispersion of individuals on their territory in different possible visitor configurations, to complement measures of inter-individual distances, for different spatial scales, and identify whether specific patterns exist.

Model and study site

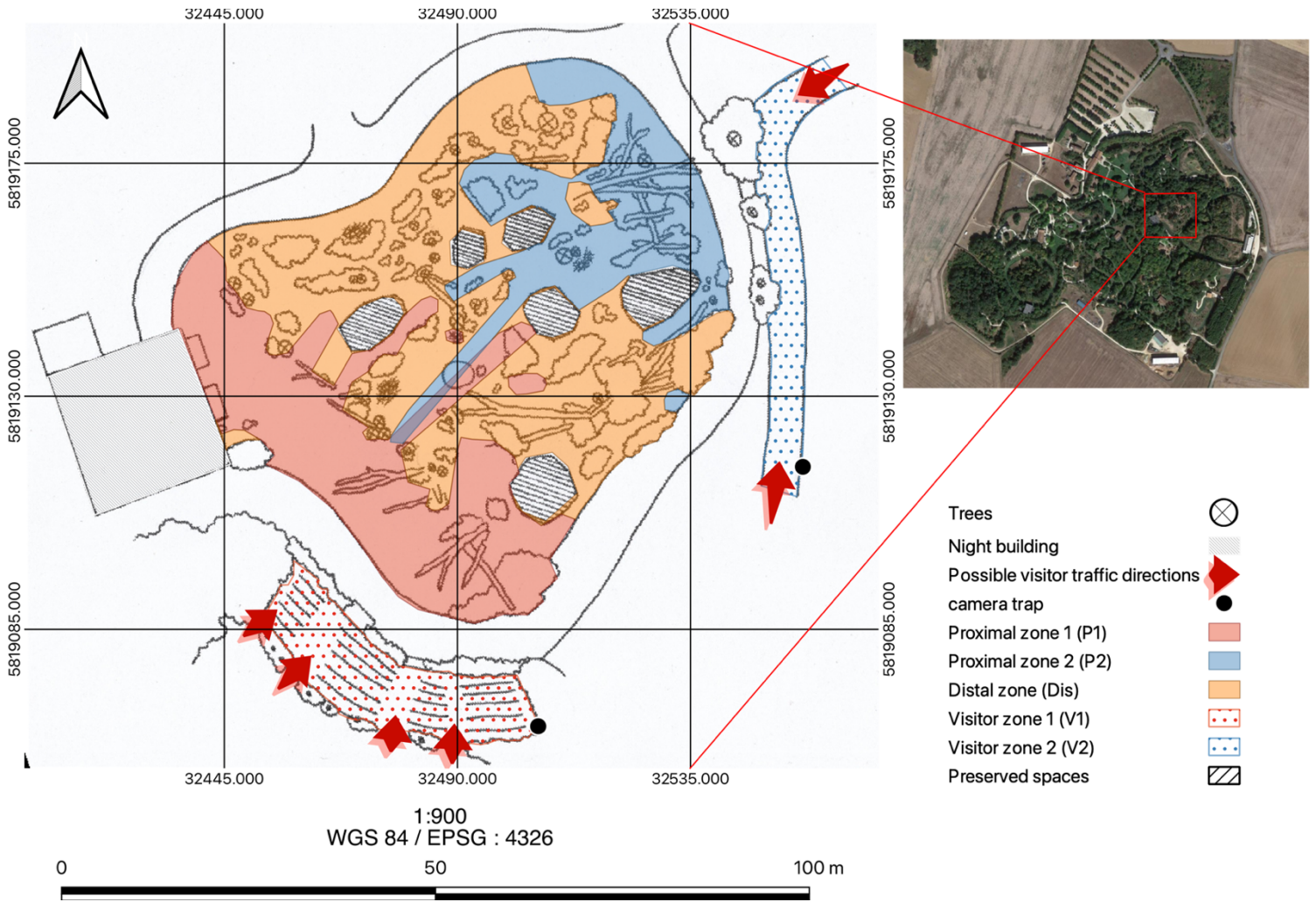
This study was carried out on a family group of Western Lowland Gorillas (*Gorilla gorilla gorilla*) of 10 individuals (see **Table 1**). This group is housed at La Vallee des Singes, in the Vienne (Romagne, France), one of the only zoos in Europe to exhibit only primates. This park has become a benchmark for zoological park research, thanks to its configuration with no cages or barriers, with naturalistic enclosures and as few primate - keeper interactions as possible. The gorillas were observed in their outdoor space, a largely wooded island with a natural appearance covering an area of around 3,700 m², with no structural enrichment and bounded by a canal filled with water. The enclosure also includes inner lodges of around 150 m² to which the individuals did not have access at the time the observations were made. Water was available ad libitum and the gorillas were fed during public sessions 4 times a day during the summer season from May to August (11:15, 14:00, 15:30 and 17:00). The group is very stable and the last individual to join the group, in 2015, was Hakuna (Ha), an adult female.

Table 1 Composition and characteristics of the Western Lowland Gorilla (*G. gorilla gorilla*) group at La Vallee 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 (female > 8 years, male > 12 years), Sub-Ad sub-adult (female 6-8 years, male 6-12 years), Inf infants (0-6 years), M male, F female. Yaounde (Ya) the dominant silverback has been highlighted in bold followed by a *.

Figure 1. Diagram of the Gorilla enclosure at La Vallée des Singes (France) showing the different zones used for the study.



Zones P1, P2 and Dis were determined empirically after 3 weeks of observation. An initial sketch of the proximal zones was drawn on the base map by defining the part of the environment visible from the two possible visitor access zones (V1 and V2). They were initially underestimated, then the precision of these zones was refined when an individual was still visible even though he was supposed to be in the non-visible zone (Dis).

The boundaries of zones V1 and V2 were determined according to whether or not it was possible to observe the individuals from the paths and observatories/grades available.

The preserved areas correspond to portions delimited by a small fence to prevent individuals from eating the young shoots and allow the new young trees to grow.



Figure 2.

a) point of view of visitors (V2) on zone P2, b) point of view of individuals from zone P2 to zone V2, c) point of view of visitors (V1) on zone P1, d) point of view of individuals from P1 to zone V1.

Material and method – data collection

Individual data

To be able to relate the environmental variables directly to those relating to visitors, the exact position of all the individuals were determined on their territory at the same time. From these coordinates we will be able to define the effect of these different variables on the distance between each individual and on the probability of their presence in the 3 zones of the territory (see Figure 1).

Initially we expect the presence of visitors to lead to a more frequent presence of individuals in the distal zone (Dis). As it is difficult to estimate the part of the territory in which individuals are unable to see visitors, we estimate that this part of the territory overlaps with the zone that is also never visible to visitors. We therefore hypothesize that if visitors do indeed have a disruptive effect on gorilla use of the territory, then it is likely that the gorillas make greater use of the area where they cannot see them and that, this area (Dis) then acts as a “retreat zone”, as described by Anderson *et al.* (2002) or Cairo-Evans *et al.* (2022).

This retreat to the Distal zone should therefore lead to a spatial contraction of the group in the presence of visitors because of the reduced usable space. This should have an effect of reduction on the distance between individuals and on the number of their occurrences in the proximal zone.

To achieve this, observations were made on the roof of the building (see **Figure 1**), giving an overall perspective of the whole area. The position of all visible individuals was plotted on the base map at regular 5-minute intervals. All of this was spread over 4 sessions during the day, with 10 measurements taken per session according to the following schedule (**Table 2**) over a period of 18 days, the dates of which were defined randomly over a period of 38 days between 30/07/2022 and 05/09/2022, giving a total of (n=722) observations.

Table 2 Planning of data sampling sessions.

| for each sampling day | |
|-----------------------|---------------------|
| with visitors | without visitors |
| 1 morning session | 1 morning session |
| 10:20 – 11:10 AM | 09:30 – 10:20 AM |
| 1 afternoon session | 1 afternoon session |
| 03:50 - 04:40 PM | 05:10 - 06:00 PM |

For each session, the position of the 10 individuals was screened at 5-minute intervals. For the two afternoon sessions, each observation was spaced 10 minutes apart from public feeding, to give the individuals time to resume normal activity.

It should be noted that the total percentage of individuals not seen over the entire study corresponds to only 6.49%. Observations were carried out during the high season to accentuate the potential visitor effect.

All the points positioned on the map were plotted on a digital version of the same base map and georeferenced using QGIS. From the distance matrices obtained, we determined the following values for each observation session:

- Average distance between all individuals (DMOY)
- Average distance between the silverback and the other sub-adult/castrated adult males (DMM)
- Average distance between silverback and females (DMF)
- Average distance between females (DFF)
- And the average distance between females and their young (DFJ)

When two individuals were observed in direct contact, the type of interaction was noted to establish a potential difference in the nature of inter-individual interactions depending on the presence or absence of visitors. In this situation a single point was placed on the physical map to optimize the speed of measurement, but two points were placed superimposed on QGIS (with different IDs for the two individuals to facilitate legibility and analysis) with a maximum distance between the points of 0.01 m to translate the direct contact between individuals numerically.

By knowing the position of the individuals, for each observation, we were able to determine:

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

Visitor data

To quantify the number of visitors present around the enclosures, only the density or position of visitors was taken into account in previous studies (see for example Thompson 1976, Glatston *et al.* 1984, Chamove *et al.* 1988, Lewis *et al.* 2020). In order to accurately measure the different variables specific to visitors, two cameras were used to film the entirety of the two portions of the zones used by visitors (see V1 and V2 in **Figure 1**) during the observation sessions. After each sampling day, the recorded videos were processed to obtain the following values for each observation (with n= 60h of recording/visitor zone):

- V1T/V2T: the number of visitors present in the two zones at time T when we recorded the position of the individuals on the map.

- V1Max/V2Max: the maximum number of visitors present simultaneously in each of the two zones during the 5-minute interval between two measurements, i.e. 5 minutes before each point was marked (a measurement was also taken 5 minutes before the first point of each session was collected).

- V1N/V2N: the number of new visitors who passed through zones of interest V1 and V2 in the 5-minute interval between two measurements.

- V1i/V2i: the type of crowd present during the 5-minute interval between two measurements (two levels: active/passive, where active corresponds to the fact that during the interval at least 1 visitor attempted to interact directly with an individual using words or gestures).

The V1i/V2i values were not used in the analysis because they only corresponded to (n=7) observations. On the boxes containing the video device it was indicated that this equipment was used for recording and was part of a study and very little direct interaction from visitors was observed during the sampling period. It is important to note that during the video recordings the framing was set up in such a way as to capture as few faces as possible or far enough away not to be identified. After counting, all the videos were deleted. The location of these video devices can be seen in **Figure 1** and their point of view can be seen in the appendix (**Figures 13 and 14.**).

Environmental data

As we saw earlier, environmental variables are important to measure because they can be very good predictors of individual behavior. Temperature, precipitation, or strong gusts of wind could significantly reduce the occurrence of individuals in proximal zones, which are more exposed to climatic hazards than distal zones. This could affect the structure of the social network by influencing the distance between individuals. Thus, for each observation of the gorilla group, values corresponding to different climate indicators are associated.

These data were collected using 3 HOBO (Pendant Temperature/Light 64K Data Logger) probes placed in fixed locations (on the roof of the building and in 2 shaded locations inaccessible to visitors) and averaged to obtain temperature data.

To complete these measurements, data from 3 weather stations near the park (BRUX; 46°16'32.0 "N 0°11'25.0 "E, CIVRAY; 46°09'37.0 "N 0°17'55.0 "E, LUSIGNAN 46°25'04.0 "N 0°07'10.0 "E) were averaged to obtain information on each observation:

- Relative humidity (%)
- Wind speed (Km/h)
- Precipitation (mm)

It should be noted that the values corresponding to precipitation were not used in the analysis because the study period was very dry, corresponding only to (n=3) observations and only 0.1 mm.

Data analysis

Structure of the social network and nature of interaction

Inter-individual distance

We used generalized linear models (GLM) with the different classes of inter-individual distances described above (*DMOY, DMM, DMF, DFF and DFJ*) as response variables. These models consider the different visitor variables for the two zones (V1) and (V2) and their interactions, as well as environmental variables and the time of day. The day of observation was used as a random factor to take into account repeated observations on the same group of individuals. Some response variables show a slight asymmetry with a straight tail but the QQplot and mean/median deviations suggest reasonable symmetry. Therefore, a Gaussian or Gamma distribution was used to fit the count data.

Social Network Analysis (SNA)

Information on the distance between individuals is not sufficient for a detailed analysis of the visitor effect on social structure and interactions between individuals. To do this, we analysed the social network of the gorilla group of interest.

Establishing social networks makes it possible to visualise relational structures, to quantify interactions between individuals and to identify those who play a key role in group dynamics. To do this, we create graphs in which each gorilla is represented by a point element (node) and the interactions between each of them are represented by links (bridges).

Here we have used undirected links where the interaction is said to be symmetrical, as opposed to asymmetrical interactions where the action is directed from one individual to another (e.g. "follows", "hits", "influences", etc.). The aim here is to represent on a graph the quantity or absence of interaction between each gorilla. To do this, each bridge is assigned a "weight" corresponding to a value frequently used for this type of SNA analysis: the Simple Ratio Index (SRI). This index, as described by Rose & Croft (2015), is defined such that for each possible pair of individuals a and b:

$$SRI = \frac{x}{x + Y_{ab} + Y_a + Y_b}$$

Where x = strength of association (number of times a and b were observed together, here in contact or < 3 m apart), Y_a = only a was observed, Y_b = only b was observed, Y_{ab} = a and b were observed separately (here not in contact or > 3 m apart).

Four networks were created to study differences in proximity and contact between individuals. Two networks were constructed based on direct interactions (gorillas are in contact), while the other two were based on proximity (gorillas are within 3 meters apart). To enable direct comparison, each type of network (contact and proximity) was created in the presence and absence of visitors. This approach makes it possible to analyze how interactions and

proximity between individuals can be influenced by the presence of visitors, highlighting their direct impact on social relationships within the group studied.

Nature and occurrence of interactions

If we follow the idea mentioned above of a decrease in the distance between individuals due to environmental conditions or visitors, then the occurrence of each type of contact between individuals should increase in the presence of the public.

During the sampling, as soon as two individuals were observed to be in contact, the type of contact was recorded along with the pair of individuals concerned, and all the contacts observed were listed in **Table 3**.

| Type of contact | Signification |
|--------------------|--|
| Eating wood branch | At least two individuals eat together the leaves of the same cut branch, placed in their territory in the morning by a caretaker. |
| Feeding | An adult female breastfeeding one of the group's infants |
| Fighting | expression of all agnostic behaviour directed from one individual to another or to each other. e.g. hitting, chasing, pinching |
| Grooming | expression of all comfort behaviours directed from one individual towards another or mutual. e.g. rubbing, lounging, embracing, delousing |
| Manipulating traps | at least two individuals are observed on the ladders leading to their inner lodges, trying to open or strike the traps allowing entry |
| Moving | one individual carries another on its back to move across the territory |
| Playing | Expression of all play-related behaviours directed from one individual to another or to each other, e.g. chasing, wrestling, spinning or tickling. |
| Resting | at least two individuals are observed resting seated or lying down together without expressing any other comfort behaviour and without at least one of the two individuals being asleep. |
| Sleeping | at least two individuals are lying asleep next to or on top of each other. |

Table 3. List of contact types observed during the study.

We then carried out a descriptive analysis evaluating the occurrence of observations of different types of contact. This will enable us to determine whether the presence of visitors plays a role in the type of interactions observed between the gorillas.

Eigenvector centrality

Eigenvector centrality is an important indicator that can be extracted from a social network analysis. This centrality makes it possible to directly assess the influence of a node (an individual) within the network by taking into account the number of direct connections it has, as well as the direct connections of its neighbours. So an individual will have a high centrality if he is connected and interacts a lot with other individuals, who are themselves important in the network. This makes it easy to identify the key individuals who will play a crucial role in the structure of the social group. On the other hand, if this centrality value is low, it will highlight individuals on the fringes of the network who interact very little with other individuals.

If following the work of Létang *et al.* (2020), the two adult males and castrated sub-adults (Djo and Maw) should occupy a relatively important position and consequently have a high centrality value relative to the other adults in the group because of their potential interaction with all the age and sex classes.

It goes without saying, given the age of the children in the group, that their position in terms of centrality should be very high. In fact, as they are still very keen to have

contact with their mothers and to interact a great deal with the other juveniles, it is highly likely that all the youngsters will have a very high centrality value, which is potentially inversely proportional to their age. The centrality of the young in the overall network is also a reflection of the many connections between neighbors, which may reflect two things. The first is that females also interact a great deal with each other, which seems logical if we extend the results obtained by Létang *et al.* (2020) beyond 6 months post-partum, indicating more female-female and female-young interactions than interactions with the silverback or other adult males. The second is that all these elements indicate that older individuals and silverbacks should be on the fringes of the overall network and therefore have lower centrality values. At the level of the group as a whole, if individuals interact more in the presence of visitors, it is possible that we will find significant differences in the importance of certain individuals within the network, and consequently a potential impact on the average centrality of the eigenvectors.

We first performed several Student's t-tests for paired data to evaluate potential differences in the average centrality of the eigenvectors of individuals in the presence and absence of visitors in the proximity contact networks. Then we will evaluate the evolution of the centrality values for each individual for the two types of network.

Personality traits

Inter-individual variations in behavior can considerably affect the place of individuals in a social network or the way they use their habitat in response to the presence of visitors. Not to take them into account would be to miss out on valuable information that will probably make it possible to explain certain results obtained at a later stage (in particular the centrality of eigenvectors or occurrences in each type of zone).

To avoid a subjective and abstract view of the personality of individuals based on the empirical experience of the observer, we decided to quantify the main character traits by following the protocol described by Gold & Maple (1994). Four caretakers, all of whom had been working with the group of interest for more than a year, individually filled in evaluation forms (see factors and their loadings in appendix), giving each personality trait listed a score from 1 (unrepresentative or non-existent trait) to 5 (highly representative trait). Each of these traits was then grouped into 4 main categories of personality aspects to facilitate analysis: Extroverted, Dominant, Fearful, and Understanding. For example, we would expect to see more of an extrovert in the proximal zone in the presence of visitors than a fearful individual. Similarly, we would not expect to find an understanding individual involved in many agnostic interactions compared with an individual expressing dominant behaviors.

Spatial distribution and habitat use:

presence of individuals in the Proximal and Distal zones

To assess the effect of visitors on gorillas' use of their habitat, we decided to look at this issue in terms of zones exposed/not exposed to visitors. We studied the presence and absence of individuals in these zones by measuring them directly in relation to variables that could induce changes, namely environmental and visitor-related variables. This study site was particularly relevant for studying this aspect of the visitor effect, as the area is bordered on both sides by an exhibition zone, making it possible to track the movements of individuals according to the presence or absence of the public in one or both of the visitor zones simultaneously.

Initially we sought to model changes in the number of individuals present in Proximal Zone 1 (nP1) as a function of environmental and visitor variables. We also took into account the time of day, which, according to observations, seemed to be an important predictor of the use of the space. We envisaged that high temperature, wind or humidity would negatively affect the presence of individuals in proximal zones, which are more open and exposed to climatic hazards, to the benefit of distal zones with vegetation cover. However, we expect that at least one of the visitor variables will have a significant effect on the presence of individuals in these exposed areas, even when the climatic variables are taken into account, to the benefit of the distal area, which provides cover for visitors.

The count data for nP1 exhibited overdispersion, so Poisson regression might have been inappropriate as it would underestimate the standard error of the coefficients and lead to overly narrow confidence intervals and biased p-values. We then used a regression model with a negative binomial distribution using the sampling day as a random factor to process the count data, taking into account the repetition of observations of the same group of individuals. This procedure was replicated for the counts of individuals present in Proximal 2 and Distal zones.

Exposure tolerance index (IT)

The exposed/unexposed zone approach directly associated with the different possible configurations of presence and absence of visitors in the two zones V1 and V2 enable us, to our satisfaction for the first time, to quantify for each individual the extent to which they accept or do not accept being exposed to the sight of visitors in each of the proximal zones.

Tolerance is an interesting indicator in its own, even more when considering in relation to the individual data acquired during this study. We would expect an older individual to have a fairly low tolerance in the proximal zones due to his years of experience of exposure to visitors, unlike a very young individual for whom the audience effect and natural curiosity should be reflected by a higher tolerance to exposure. Similarly, we would expect a more introverted individual to have a lower tolerance to exposure than an extroverted individual.

This exposure tolerance is determined in the form of an index, corresponding to a relative ratio between the different observation frequencies, normalised as a function

of the total number of observations of an individual of interest per zone, thus making this index comparable between the different individuals in the group.

Thus, for Proximal zone 1, tolerance is quantified as follows:

$$ItP1 = \frac{\left(\frac{(a + d)}{m1} \right)}{\left(\frac{(b + c)}{m1} \right)}$$

Where *a* = number of observations of the individual in zone P1 without any visitors, *b* = number of observations of the individual in zone P1 with visitors present in V1 and V2, *c* = number of observations of the individual in zone P1 with visitors present in V1 only, *d* = number of observations of the individual in zone P1 with visitors present in V2 only and *m1* = total number of observations of the individual in P1.

An ItP1 value > 1 corresponds to a higher frequency of observation of the individual of interest in Proximal zone 1 when there are no visitors or only in V2, i.e. on the other side of the territory, compared with when there are visitors all around the territory or only in V1. This can be translated as a low tolerance of exposure to visitors in this zone.

A value of ItP1 = 0 indicates that the presence of visitors has no influence or a neutral influence on the frequency of observation of the individual in P1.

A value of ItP1 < 0 corresponds to a higher frequency of observation of the individual of interest in Proximal zone 1 when there are visitors all around the territory or only in V1 compared with when there are no visitors or only in V2. This can be translated into a high tolerance of exposure to visitors in this zone.

Similarly, for Proximal zone 2:

$$ItP2 = \frac{\left(\frac{(e + h)}{m2} \right)}{\left(\frac{(f + g)}{m2} \right)}$$

Where *e* = number of observations of the individual in zone P2 without any visitors, *f* = number of observations of the individual in zone P2 with visitors present in V1 and V2, *g* = number of observations of the individual in zone P2 with visitors present in V2 only, *h* = number of observations of the individual in zone P2 with visitors present in V1 only and *m2* = total number of observations of the individual in P2.

An ItP2 value > 1 corresponds to a higher frequency of observation of the individual of interest in Proximal zone 2 when there are no visitors or only in V1, i.e. on the other side of the territory, compared with when there are visitors all around the territory or only in V2. This can be translated as a low tolerance of exposure to visitors in this zone.

A value of ItP2 = 0 indicates that the presence of

visitors has no or a neutral influence on the frequency of observation of the individual in P2.

A value of $ltP2 < 0$ corresponds to a higher frequency of observation of the individual of interest in Proximal zone 2 when there are visitors all around the territory or only in V2 compared with when there are no visitors or only in V1. This can be translated into a high tolerance of exposure to visitors in this zone.

Retreat index (RI)

In addition to knowing the extent to which individuals tolerate or do not tolerate the presence of visitors in proximal zones, it is also interesting to see whether the absence of individuals in proximal zones is to the benefit of distal zones (if we follow the hypothesis that the latter constitute a proven "retreat zone"). To do this, we calculate a relative ratio between the different observations of each individual of interest in distal zones without and with visitors. We then compare the average of the indices obtained for each possible visitor configuration with a Wilcoxon signed-rank test to determine whether the presence of visitors in V1, V2 or both simultaneously significantly affects the presence of individuals in the distal zone.

We calculate :

$$\frac{\left(\frac{i}{m3}\right)}{\left(\frac{j}{m3}\right)} \quad \frac{\left(\frac{i}{m3}\right)}{\left(\frac{k}{m3}\right)} \quad \frac{\left(\frac{i}{m3}\right)}{\left(\frac{l}{m3}\right)}$$

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

A retreat index Ri equal to 1 would indicate that the presence or absence of an audience has no impact on the presence of the individual in the distal zone.

An index Ri less than 1 indicates that the individual is more present in the distal zone when the public is present (in V1 or V2 or both simultaneously) than when the public is absent, and therefore indicates a withdrawal in this zone.

An index Ri greater than 1 indicates that the individual is more present in the distal zone when there are no visitors than when there is a public present (in V1 or V2 or both simultaneously) and indicates that there is no withdrawal effect in the distal zone.

Spatial dispersion patterns

We have the exact location of all the individuals for the different possible configurations of presence and absence of visitors. During the observations, we noted that the presence of visitors could have an impact on the positioning of individuals, thereby creating dispersal patterns at the scale of the territory.

In fact, at the beginning of the morning sessions without visitors, we observed that the individuals used a large part of their territory, unlike the last sessions, a little later in the morning, where clusters of individuals seemed to form frequently. To check whether we could generalize the spatial dispersion models for different configurations of presence or absence of visitors, we extracted the coordinates of individuals in four situations: without visitors, with visitors only in zone V1, with visitors only in zone V2 and finally with visitors in zones V1 and V2 simultaneously.

To analyse these data, we used a function called Ripley's L function, proposed by Besag in 1997 (Besag 1997) with the Spatstat package under R. This function is a standardised adaptation of the original function, Ripley's K function, as introduced by Ripley B. D. in 1976 (Ripley 1976) and developed in more detail a few months later (Ripley 1997). This function is used to evaluate the distribution of points in a given space and to identify any dispersion patterns. Its normalisation makes it possible to make the models more linear and to clarify their interpretation later on. The advantage of the value obtained by this function is that it is estimated as a function of a distance scale "r", enabling dispersion patterns to be assessed on both a large and a smaller scale.

To our knowledge, this is the first time in an ecology study that this function has been used to describe the spatial dispersal of individuals directly, rather than at specific points in the environment such as for example nesting sites, plants ecology or climatic events (see for example Lynch & Moorcroft 2008, Turner 2009, Law et al. 2009, Kiskowski et al. 2009). Fixing the position of individuals in space for comparison between different situations makes it possible to apply these functions originally described for immobile events.

The L(r) function is estimated as :

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

Where $K(r)$ is estimated as :

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

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

The Ripley function is generally used to compare the actual spatial distribution of points with a random spatial distribution. If $L(r)$ is greater than the reference line ($L(r) > r$), this indicates spatial aggregation of points at this scale. If $L(r)$ is less than the reference line ($L(r) < r$), this suggests spatial repulsion. If $L(r)$ closely follows the reference line, this indicates a random or regular spatial distribution of points. To ensure that the interpretation is not purely

graphical, a 95% confidence interval is defined using a Monte Carlo procedure. If the curves of interest lie outside this interval, we can then consider a significant deviation from the reference line, which defines a random distribution.

Results

Inter-individual distance

The presence of visitors in zone V1 only had a significant effect on the distance between Yaounde and the other two castrated males (DMM). The number of new visitors passing by (V1N) and the number observed at the time of the position survey (V1T) slightly reduced this distance (respectively Est -9.589e-04, P= 0.0001 and Est -7.617e-04, P= 0.025), whereas a simultaneous maximum number (V1Max) increases it slightly (Est 9.417e-04, P= 0.006). On the other hand, the presence of visitors in zone V2 only has a significant effect on the distance between females and their respective young (DFJ). (V2Max) increases this distance (Est 2.460e-03, P= 0.023) and (V2T) decreases it (Est -3.232e-03, P= 0.003). The presence of visitors in both zones V1 and V2 simultaneously revealed no significant effect on the different classes of distance between individuals, with the exception of the interaction (V1N*V2N), corresponding to all new visitors passing all around the territory on either side. This interaction decreases the average distance between individuals (DMOY) (Est -0.027735, P= 0.018) and increases the (DMM) (Est 9.338e-05, P= 0.007).

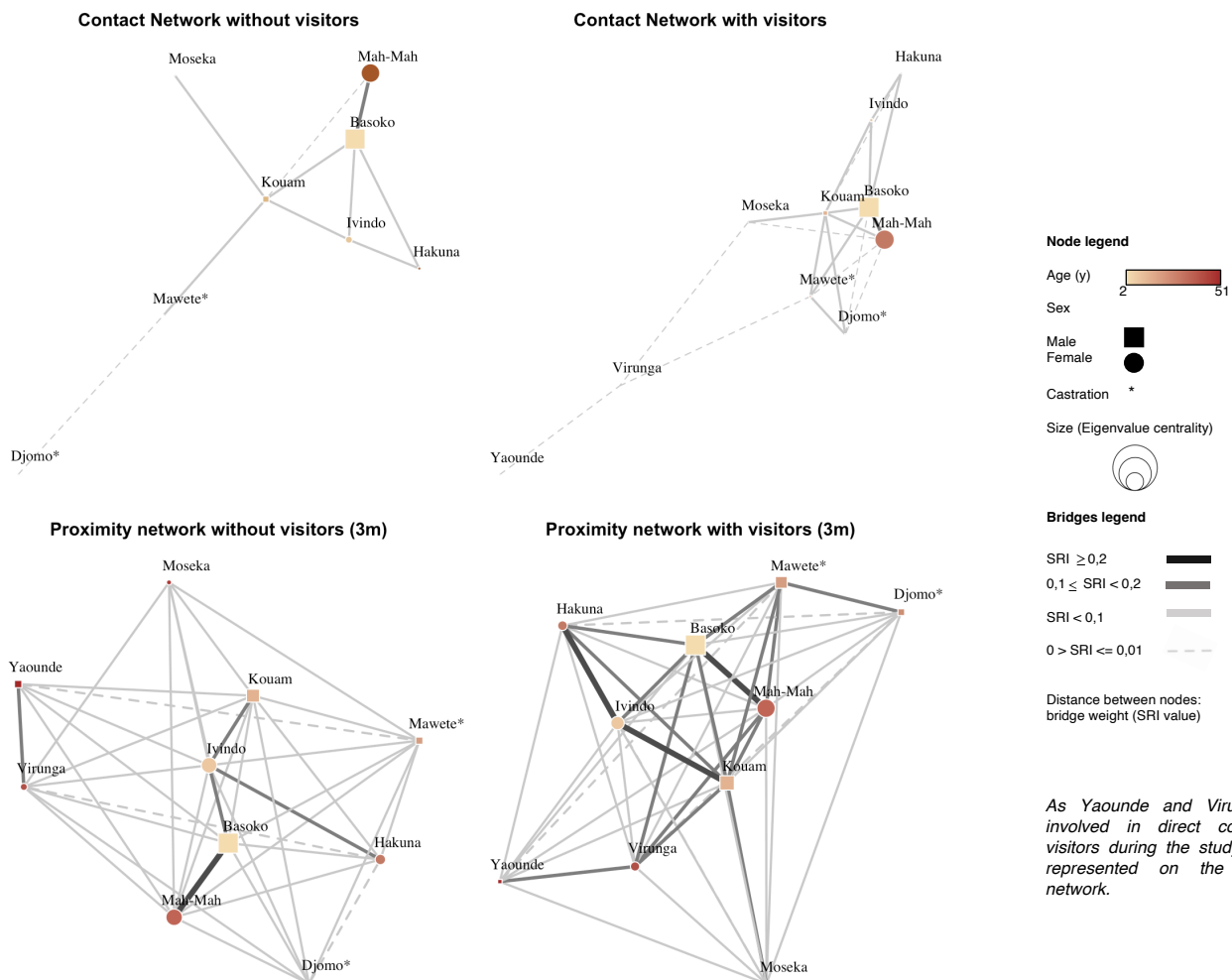
Environmental variables also significantly affect the distance between individuals. Wind, humidity and temperature, at whole-group scale, reduce the mean distance between individuals (DMOY) (Est -0.197554, P= 0.015 /Est -0.074413, P= 0.016 /Est -0.640310 P= 5.01e-06). In more detail, however, humidity increases (DMM) (Est 2.893e-04, P= 0.0001) and temperature increases (DMM) (Est 1.383e-03, P= 5.78e-05) and the mean distance between adult females (DFF) (Est 2.303e-03, P= 0.0001).

Finally, time of day is the last significant predictor of distance between individuals. In contrast to the morning, individual (DMM)(Est 8.939e-03, P= 2.41e-05), (DMF) (Est 1.146e-02, P= 0.003), (DFF) (Est 1.034e-02, P= 0.005) and (DFJ) (Est 2.541e-02, P= 0.0002) are slightly higher in the afternoon. However, when all the individuals in the group are considered, the average distance between individuals (DMOY) is about 5.28 meters lower than in the morning (Est -5.280682, P= 1.13e-12).

Social Network Analysis (SNA)

Using a quantitative approach, we calculated the difference between the number of contacts in the presence and absence of visitors. The distribution of values, according to the Shapiro tests obtained, does not follow a normal distribution (P= 1.562e-07), even after removing the Mah-mah (Ma) - Basoko (Ba) interaction (P= 0.003) which, as can be seen in **Figure 3**, interacts much more than the other binomials. However, as the conditions for

Figure 3. Diagram of the 4 social networks of contact and interaction of the gorilla group at La Vallée des Singes (France).



a non-parametric test are met, we use a Wilcoxon signed-rank test for paired data (or Wilcoxon signed-rank test) with a p-value = 9.199×10^{-5} ($P = 0.0001$ without (Ma) - (Ba)). This indicates a significant increase in the number of contacts in the presence of visitors compared with no visitors.

As female-infant interactions appear graphically as the pairs that interact the most, we performed a Mann-Whitney U test to compare the difference in the number of interactions with and without visitors between these pairs of interest and the other possible pairs. The results obtained (p-value = 0.042) indicate that the difference in the number of contacts in the presence and absence of visitors is also significantly higher between females and their infants compared with the other types of possible pairs.

The same analysis is carried out for the differences in occurrences close to the place of direct contact. Here again the distribution is not normal (p-value 9.73×10^{-7}) and (p-value 0.005 without the (Ma) - (Ba) pair). The Wilcoxon signed-rank test gives a p-value = 9.616×10^{-9} (and $P = 1.422 \times 10^{-8}$ without (Ma)-(Ba)). This also indicates a significant increase in the proximity of individuals in the presence of visitors compared with without visitors. Similarly, the Mann-Whitney U test gives a p-value = 0.026 indicating that proximity in the presence and absence of visitors is also significantly higher between females and their offspring compared to the other possible pairs.

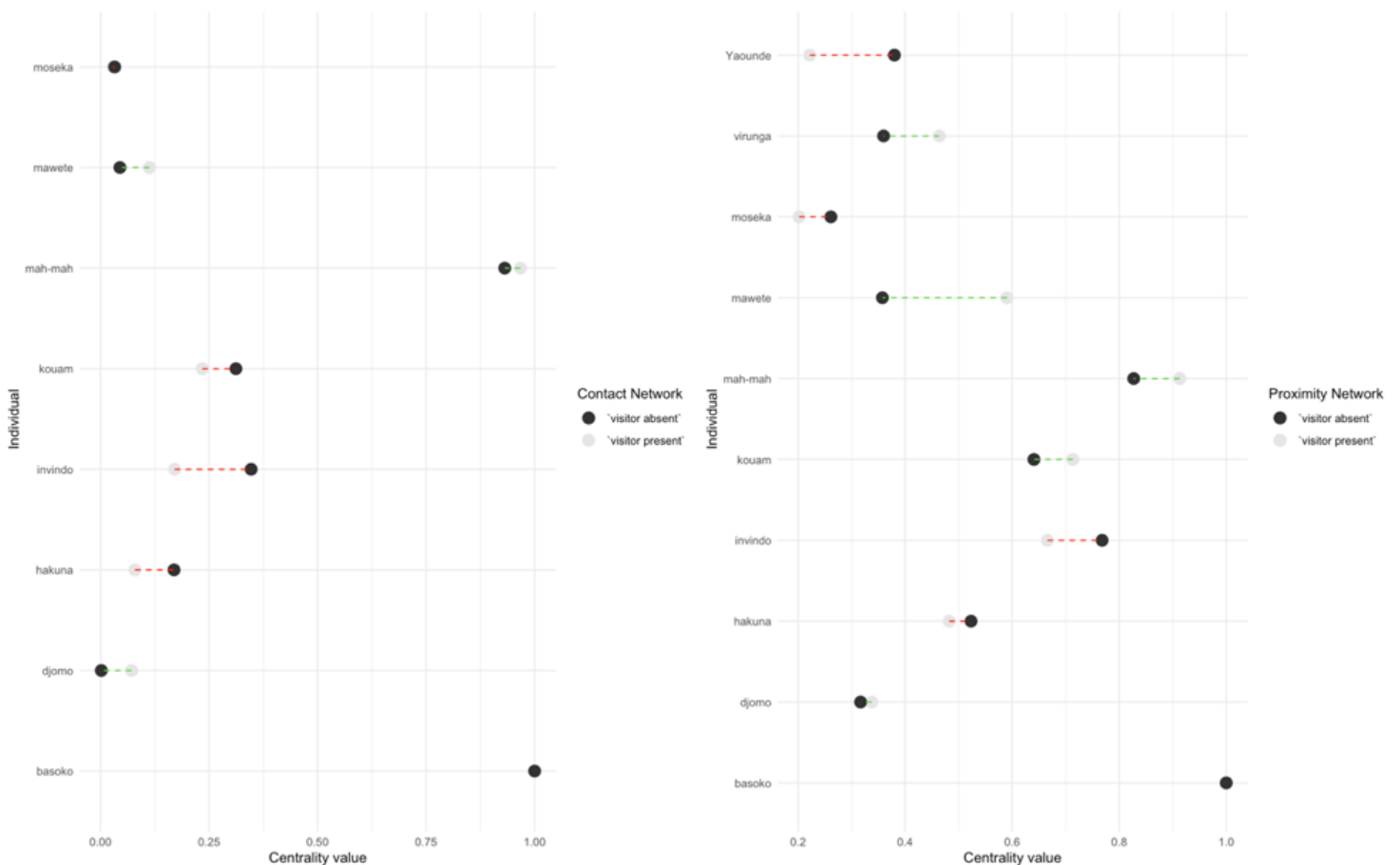
Eigenvector centrality

Student's T-test for paired data revealed no significant difference in the average value of centrality in the presence and absence of visitors for contact networks (Pval 0.499) or proximity networks (Pval 0.675). This indicates that, on average, the importance of individuals within networks was not significantly impacted by the presence of visitors.

We have nevertheless represented the evolution of the centrality of each individual according to the presence or absence of visitors. As Yaounde and Virunga were not observed in contact without visitors, they are not visible in the first part of **Figure 4**. The individuals with the lowest centrality in the contact networks are Djomo, Mawete and Moseka, i.e. the two castrated males and the second older female, and these values change little in the presence of visitors. The individuals with a higher value are Mah-mah and his son Basoko, and this value is much higher than that of the other individuals. There was little variation in the centrality of the contact networks, apart from a drop in the presence of visitors for two of the juveniles: Kouam and Ivindo, and for Hakuna, another adult female.

When visitors are present, Yaounde and Moseka have a lower centrality in the proximity networks, but Mah-mah and Basoko still have the highest centrality value. Unlike the contact networks, these proximity networks show greater variation, especially for intermediate values of centrality in the presence of visitors, especially for Virunga, Mawete, Kouam, Ivindo and Mah-mah.

Figure 4. Comparative representation of the centrality of the eigenvectors of individuals in the gorilla group at La Vallée des Singes within the contact and proximity networks in the presence and absence of visitors.



The centrality values of each individual are represented in black in the absence of visitors and in grey in the presence of visitors. A dotted red line indicates a decrease in centrality with visitors, while a dotted green line indicates an increase in centrality with visitors.

Nature and occurrence of interactions

Using a more qualitative approach to the type of contact observed between individuals, we obtained the following results shown in **Figure 5**.

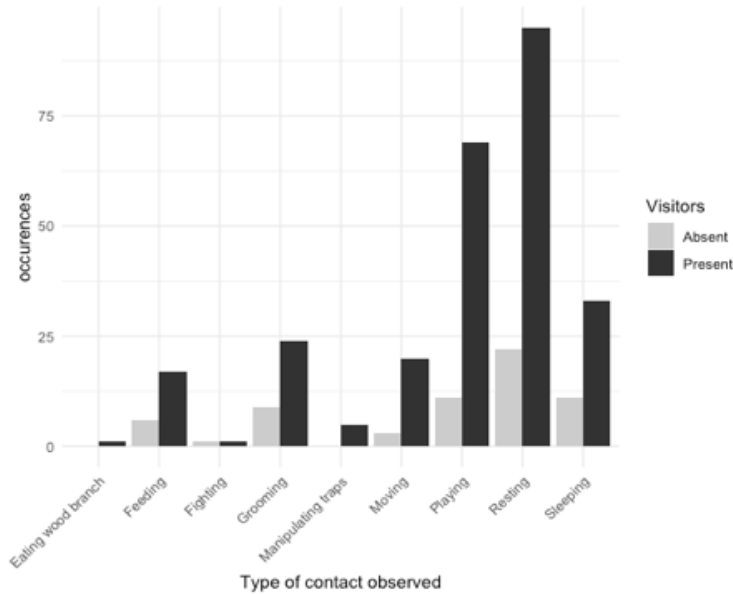


Figure 5. Occurrence of each type of contact observed in the gorilla group at La Vallée des Singes (France) with and without visitors present.

Regardless of the type of contact, the number of occurrences observed was always higher when visitors were present than when they were absent. The majority of contacts observed in this group correspond to comfort or play behaviors (Playing, Resting, Sleeping). However, certain types of contact are only observed in the presence of visitors, such as sharing a branch of wood or manipulating the building's traps. Finally, the only agonistic behavior (Fighting) was only observed once for each of the configurations.

Presence in the Proximal and Distal zones

Proximal zone 1

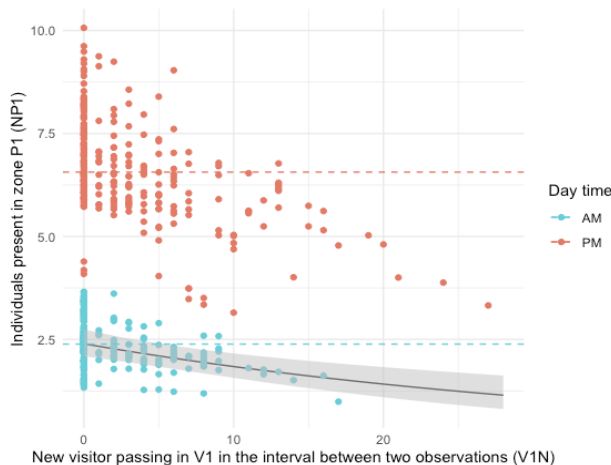


Figure 6. Graphical representation of the evolution of $nP1$ as a function of the only significant visitor variable $V1N$.

The models used highlighted the fact that the number of new visitors passing by ($V1N$) significantly reduced the number of individuals present in zone P1 (Est -0.0262284, Pr 4.92e-05) where $V1Max$ and $V1T$ showed no significant

effect (Pr 0.295 and Pr 0.727). Wind, humidity and temperature also significantly reduced the number of individuals in P1 (Pr 0.0003, Pr 0.0369 and Pr 0.035) but $V1N$ remained a better predictor for $nP1$. Finally, there were significantly more individuals, at least one, in zone P1 in the afternoon than in the morning (Est 1.09993, Pr 2e-16).

Proximal zone 2

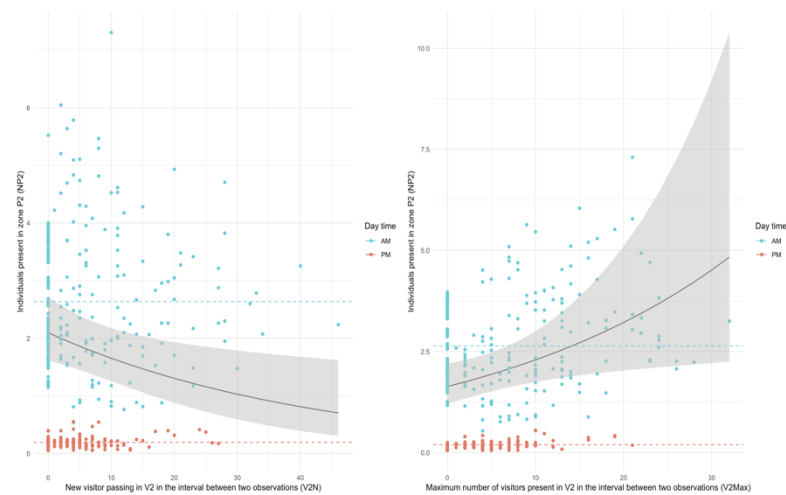


Figure 7. Graphical representation of the evolution of $nP2$ as a function of the significant visitor variables $V2N$ and $V2Max$.

On the other side of the territory, we identified that two of the visitor variables significantly affected the number of individuals present in zone P2. As for the P1 zone, ($V2N$) reduced the number of individuals in P2 (Est -0.023711, Pr 0.013) while ($V2Max$) increased it (Est 0.033926, Pr 0.017). As with P1, temperature significantly reduced the number of individuals in zone P2 (Est -0.083754, Pr 0.002). The time of day was also a good predictor, with at least 2 fewer individuals in zone P2 than in the morning (Est -2.239054, Pr 2e-16). ($V2T$) and the other environmental variables appeared to have no significant effect.

Distal Zone

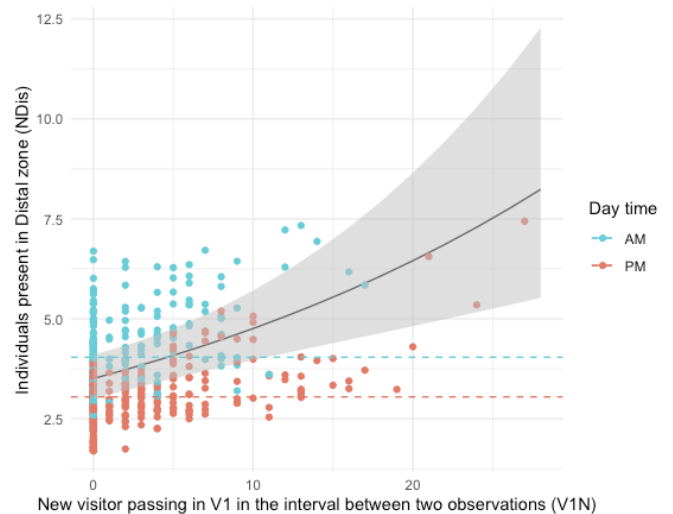


Figure 8. Graphical representation of the evolution of $nDis$ as a function of the only significant visitor variable $V1N$.

To model the evolution of the number of individuals in the Distal zone, we added the interactions of the different visitor

variables to the model in order to test a potential significant effect of these variables when acting simultaneously. However, none of the interactions appeared to be significant. Only (V1N) significantly increased the number of individuals in the Dist zone (Est 3.285e-02, Pr 0.0002). Wind also increased nDis (East 4.343e-02, Pr 9.28e-05). Once again, Md was also a good predictor, with at least 2 fewer individuals estimated in the distal zone in the afternoon than in the morning (East -2.307e-01, Pr 0.011).

Exposure tolerance index (ETI) and Retreat index (RI)

As the retreat indexes were calculated independently for the 3 possible visitor configurations, it was necessary to compare them. We used signed-rank Wilcoxon tests to compare them in pairs. The results suggest a value of RiV1V2 less than 1, indicating that individuals are more present in the distal zone when there is a public in V1 and V2 simultaneously than when visitors are absent. This points directly to a phenomenon of retreat in (Dis) zone for this visitor configuration. On the other hand, RiV1 and RiV2 values are >1, indicating that the individual are more present in the distal zone when there are no visitors than when there is a public present (in V1 and V2 independently) and therefore not necessarily indicating a retreat effect. By comparing the values of the three retreat indexes with Wilcoxon signed-rank tests, we were able to determine that RiV1V2 showed significant differences from RiV1 and RiV2 (Pval 0.002 and 0.002) but that there was no significant difference between the latter two (Pval 0.275).

In addition to the Retreat index (RI) values, we used the values obtained for the Exposure tolerance index (ETI) as part of a PCA with the individual data to establish potential correlations between these calculated indices and age, gender and the various character traits. To complete the graphical analysis shown in **Figure 11**, we created a correlation matrix, displaying only significant correlations determined using the cor.mtest function of the corplot package in R.

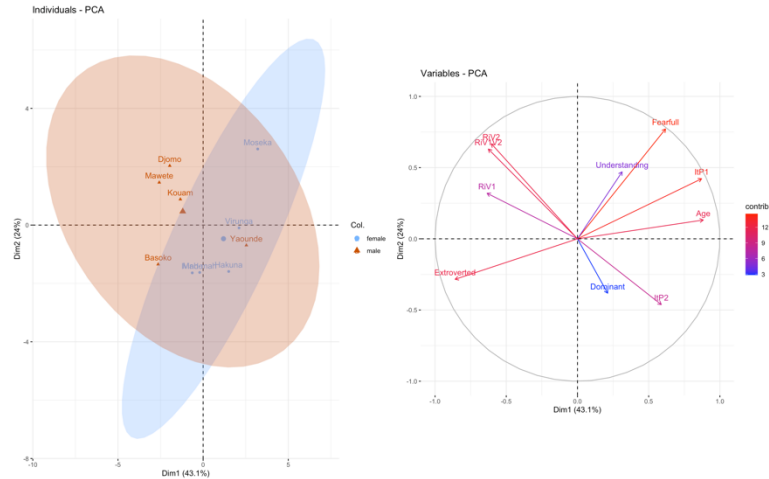


Figure 11. graph representing the different individuals and variables considered according to the two main PCA axes.

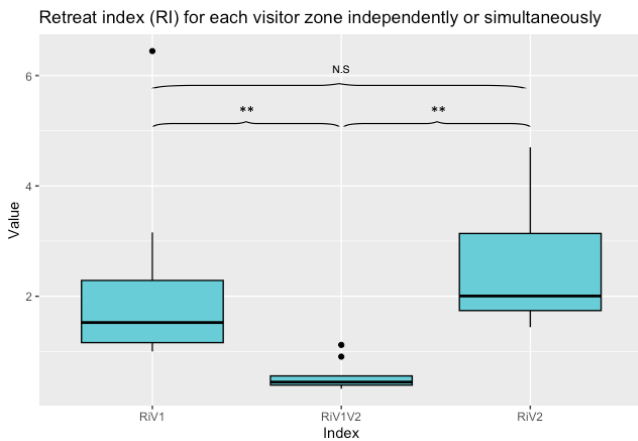


Figure 9. Boxplot of the calculated values of the 3 retreat indexes (Ri).

Visualizing this matrix (Figure 10) allows us to highlight typical individual profiles. If we focus on the main character traits, we can say that extroverted individuals are also the youngest and least fearful. Similarly, the most fearful individuals are also the most understanding and elderly. If we try to establish an individual profile by calculated index, we observe that for the 3 indices RiV1V2, RiV1 and RiV2, the youngest individuals are those with the highest value, which means that unlike the older individuals, there is no tendency to retreat into the distal zone in the presence of visitors in both zones V1 and V2 or simultaneously. Furthermore, the extraversion trait seems to be a good indicator of distal zone withdrawal, as individuals with a higher Ri value are also the most extroverted.

If we now turn to the tolerance indices, we see that the individuals most tolerant of exposure to visitors in zone P1 (ItP1) are also the most understanding, the most fearful and the oldest. These are also the most introverted individuals and those with the lowest RiV1 and RiV1V2, suggesting that they will exploit the distal zone more in the presence of the public. Similarly, for ItP2, the most tolerant individuals will be the oldest and most dominant, and those with the lowest Ri indices.

Finally, on the basis of sex, it seems that the females in the group have higher Understanding and Fearfull values, are generally older, express more dominance-related traits, and are more tolerant of exposure to visitors in both zones P1 and P2 than the males. Males, on the other hand, have higher Ri value so retreat less in the distal zone, but tend to be more extroverted than females.

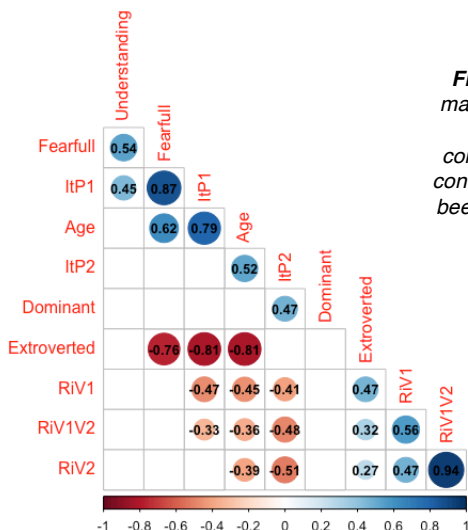


Figure 10. Correlation matrix of PCA variables (Only significant correlations with a 95% confidence interval have been displayed for ease of reading)

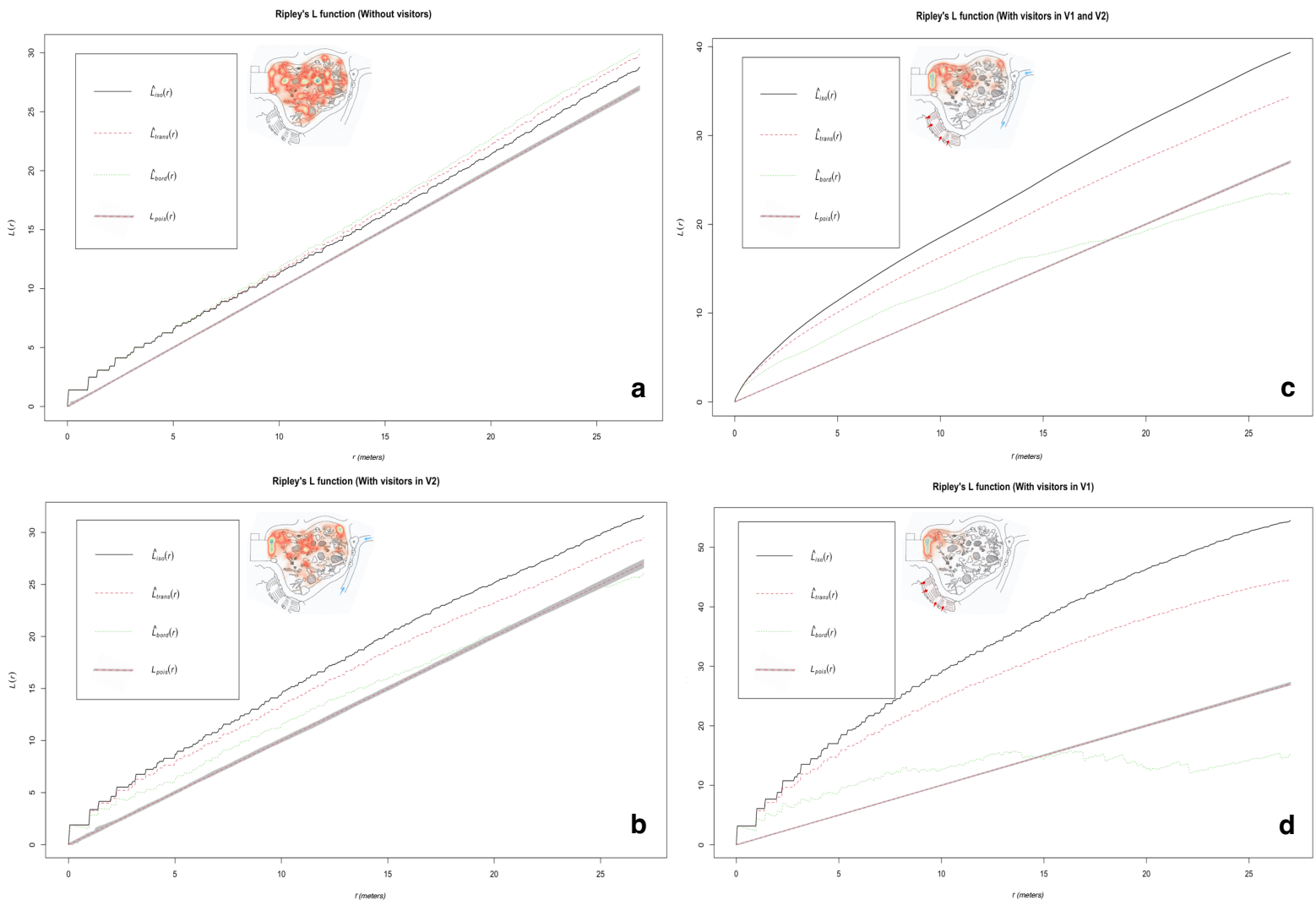


Figure 12. Graphical representation of Ripley's $L(r)$ functions in the absence and presence of visitors in zone V1, V2 or both simultaneously. The solid black curve corresponds to the actual observed distribution, the dotted red curve corresponds to a transformation where r is subtracted from the observed $L(r)$ function to examine the actual distribution of points, taking into account the distance between points, the dotted green curve corresponds to the edge correction and the dotted red line $L_{pois}(r)$ surrounded by grey corresponds to the theoretical $L(r)$ function for a poisson process, i.e. a random spatial dispersion model in defined space. To facilitate graphical interpretation, the confidence interval obtained by the Monte Carlo procedure has been added in grey around the random dispersion model. These models were generated using the Spatstat package in R, using the coordinates of the territory boundaries as the maximum distribution window.

Spatial dispersion patterns

We tested the distribution of our individuals in the 4 possible configurations of presence/absence of visitors with the Ripley model, the results of which can be seen in Figure 12. First of all, we note that all the curves corresponding to the actual distribution of points ($L_{obs}(r)$) lie above the $L_{pois}(r)$ curve and outside the confidence interval, indicating a significant tendency towards aggregation for all the configurations tested.

We'll take situation "a", with no visitor, as our baseline for comparison with the others. There is a slight but significant tendency towards aggregation, but no major deviation with a completely random distribution, nor with edge transformation and correction, and this in a linear fashion for the different distance scales. This is a quasi-random distribution situation, with a slight tendency towards aggregation and a contribution from points on the edges of the territory that is as significant as that from points in the center.

The $L(r)$ value measures the number of events (here, individual observation points) observed L at a distance r or less from a reference event, on average, compared with what would be expected with a random spatial distribution. Here, for example, without visitors (a), for a radius of 5 units ($r=5m$), there are around 6 times more observations of individuals ($L(r) = 6$) around each reference observation than would be

expected with a random distribution.

Situation b (with visitors only in V2) is the one that most closely resembles the trends seen in situation a. However, the tendency towards aggregation is almost twice as strong for all possible r values. Here, for example, $L(r=5) = 9$. Moreover, the contribution of points at the edge of the territory no longer becomes significant for larger scale values (above $r=20$).

Situation d (visitors only in V1) reflects a very strong tendency towards aggregation. On a small scale, this trend is already well beyond situation a or b, $L(r=5) = 19$ for example, and the deviation from a random distribution continues to increase on a larger scale. Once again, the contribution of points at the edge of the window is significant up to around $r=15$, then no longer significantly affects the observed distribution of points, meaning that those further from the edges contribute more to the aggregation.

Finally, situation c (visitors in V1 and V2 simultaneously) represents an intermediate situation between b and d. It shows a strong tendency towards spatial aggregation, but lies between the distribution curves observed in situations b and d. The contribution of points at the edge of the territory is once again significant on a local scale, then becomes insignificant at around $r = 18$ (i.e. still between b and d).

Discussion

We used several very different approaches to try and describe as precisely as possible the visitor effect, which is still relatively unknown today, especially in naturalistic environments. Our results suggest that the presence of visitors does play a role in how individuals interact and use their territory, but it is even more interesting to see that not all visitor variables had a significant effect. Indeed, for the most part it was only the variable (VnN) corresponding to a certain number of new people moving along the paths around the territory, which affected the distance between certain individuals, but which at group level reduced the distance between them.

An increase in this variable will also reduce the number of individuals present in the two corresponding proximal zones, and for (V1N) increase the number of individuals present in the Distal zone. The variables (VnMax) and (VnT) show some significant effects, such as increasing or reducing the average distance between certain classes of individuals, but it is interesting that it's (VnN) that has a significant effect in most cases. This is partly in response to the need to disentangle what effect the presence of zoo visitors does or does not have on gorilla behavior. It would seem, then, that for this type of naturalistic environment, large crowd movements have a more intense effect on gorillas' use of their territory than do crowds of stationary visitors. It is important to note that all environmental variables were very good predictors of the position of individuals on the territory as we expected, however contrary to the results of the study of Rose *et al.* (2020) with Black-helmeted Hornbills (*Ceratogymna atrata*), when visitor variables had a significant effect, they were more so than environmental variables.

On the other hand, having a significant effect of visitor variables in zone (V1) rather than (V2) may be interpreted by a different perception of visitors by the gorillas in these two zones. As shown in **Figure 2**, Zone (V2) is sheltered behind trees, so that the gorillas in Proximal Zone 2 can't see visitors over the whole zone, unlike zone (V1), which is wide open and exposed, so that any visitor present can be seen by the gorillas in Proximal Zone 1. Zone (V1) is also where visitors go during the day for public feedings, so it's possible that gorillas assimilate this zone more to a disturbance, or at least to the presence of visitors in general. The weaker reaction of individuals to visitors present in zone (V2) is similar to the results obtained by Blaney *et al.* (2004), where the impossibility of direct visual contact with visitors reduced aggression and stereotypy.

We tested the possibility that the distal zone, where the gorillas are never visible to visitors (and where the opposite is believed to be true), constitutes a true retreat zone where individuals can go to hide from the pressure induced by the presence of visitors. This appears to be the case, as a high value of (VnN) significantly increases the number of individuals in the distal zone. This phenomenon is confirmed by the calculation of Retreat (Ri) and exposure tolerance (It) indexes. Indeed, the individuals who will spend more time in the Proximal zone in the presence of visitors are the young gorillas, and/or the individuals

identified as the most extroverted and the least fearful, as they are associated with higher values of (Ri) and therefore no retreat phenomenon in the distal zone. The opposite is true of older, introverted, and fearful individuals.

These various Retreat and tolerance indexes seem to be very useful indicators and reflect the observed reality, but the results described for this study should be treated with caution. The interpretation of these indexes to different age classes, sex or character traits is informative but not necessarily representative of the captive gorilla population, especially as individual variation within these groups affects the results obtained. A telling example is the Exposure Tolerance Index in Proximal Zone 1 (ItP1). If we follow this analysis, the individuals most tolerant of exposure in this zone are the shyest and oldest individuals, but these results are biased by the values obtained by one female, Moseka, the second oldest female and described as the shyest of the group, who will in fact be frequently present in zone P1 but, rather than because of visitors, it is more because she is a solitary female who will seek out portions of territory where other individuals will generally be little present.

However, the scope of the results obtained is limited by the fact that the observations were carried out on 10 individuals from a single group, a replication of the calculation of these indexes to other groups of captive gorillas should, in comparison with the results obtained in the present study, attenuate the effect of inter-individual differences and enable the interpretation of the values obtained to be generalized.

Other models such as dispersion, relative variance, aggregation and indices like those of Lexis or Charlier could have been considered, but as de Freitas Alves & de Santana (2021) have highlighted, all these methods fail to take into account possible differences in distribution at different scales. In addition, other widespread methods based on distances to the nearest neighbor, such as The Clark-Evans index of clumping (CE) introduced by Clark & Evans (1954), are limited in that they only describe spatial structure at the very fine scale of the nearest neighbors (Dale *et al.* 2002), which severely limits overall interpretation in the case of strong dispersion, for example. Furthermore, Kint *et al.* (2003) argue that this index (CE) is only relevant to be applied to a distribution of points that is considered to be already aggregated before analysis.

Until now, Ripley's K and L functions, already employed in spatial ecology research, had mainly been applied to static events such as trees or climatic phenomena (Lynch & Moorcroft 2008, Turner 2009, Law *et al.* 2009, Kiskowski *et al.* 2009). However, this study marks the first use of these functions to directly analyze the movements of individuals of a moving animal species. Indeed, the spatial fixation of moving events for specific situations (in this case, the presence or absence of visitors) means that these events can be considered static, models can be applied and a global pattern of use of the given surface can be determined and compared. This new approach opens up exciting prospects for research, enabling a deeper understanding of complex spatial interactions. This is all the more relevant in captivity, where available space is easily identifiable and visibility is high.

By integrating the concepts of spatial distribution and distances between individuals in a dynamic context, Ripley's K and L functions now provide a powerful tool for exploring dispersal patterns, groupings and browsing behaviors, whether on a very fine scale, more globally or for a window defined like an enclosure.

The global phenomenon of aggregation of individuals in the presence of visitors is confirmed using Ripley models. The results obtained not only correspond to the reality observed during sampling, but also consider the preference of individuals for proximity to their building and the structures providing access to it (Ogden *et al.* 1993, Ross & Lukas 2006), thanks to the edge correction visible in **Figure 12**. The slight tendency towards aggregation, even without visitors, is normal and corresponds to one of the limits of the function: the territory is not a neutral matrix where absolutely all spaces are available, so the tendency towards aggregation may be induced by the use of certain paths between bushes and trees that are more frequently used. However, this aggregation is not synonymous with an increase in agonistic interactions. On the contrary, the vast majority express comfort or resting behaviors, with no increase in aggressive behaviors. No stereotypic or self-mutilating behaviors were observed either.

This study is a pilot project whose protocol is intended to be replicated, in line with a desire to generalize the study of the visitor effect as precisely as possible, which until now has seemed very complicated, due to the very different and numerous possible configurations of housing conditions. Replication of the proposed methodology should make it possible to attenuate individual variations, correct inaccuracies in the calculated indexes and generalize the results obtained here to the scale of the captive population. Furthermore, the absence of artificial structures or enrichment with which to interact does not seem to induce more abnormal behavior and could even be one of the elements explaining the numerous interactions between individuals here.

In future, another methodology, the radial distribution function (or pair correlation function) noted $G(r)$, may be borrowed from statistical physics. Although the latter is currently only used to describe the spatial distribution of particles in a system, and to give information on the probability of finding a particle at a certain distance from another reference particle (Stachurski 2015, Wade *et al.* 2018), it is possible to exploit this concept by using the spatial coordinates of individuals, as we do with particles in a system, to give indications on the spatial attraction or repulsion between points of interest. Similarly, the Bivariate version of this function can be used to define a class of points (for example male and female) to study the phenomena of attraction, repulsion or spatial independence between these classes more easily than with a univariate analysis.

Taken as a whole, this work nevertheless highlights the proven existence and hence the need (already called for in the study by Hashmi *et al.* in 2020) for the presence

of a retreat zone in the enclosures, acting as a buffer to visitor disturbance and allowing individuals to retreat or not from the sight of visitors if they so wish. The latter seems to be even more important for shy, introverted or elderly individuals, who seem to be more sensitive to it. However, the possibility of seeing or not seeing individuals seems to affect the "zoo experience", but there is yet no clear consensus on this subject. While some work debates the fact that visitors spend more time around an enclosure where animals are visible and active (Altman, 1998; Anderson *et al.*, 2003, Godinez *et al.*, 2013) some describe that visitors spend more time looking for individuals to observe, thus reinforcing the attraction (Philpot 1996). Others attest that viewing these animals in naturalistic enclosures induced a better perception of animals in captivity, a greater sense of well-being, higher attraction in conditions closer to nature and a more relevant educational resource for children (Melfi *et al.* 2004, Nakamichi 2007, Kutska 2009). An approach such as the one presented here, addressing the presence and absence of individuals in proximal areas and the presence of visitors, could also help assess the enclosure's attractiveness to the public present.

As the zoo environment remains in constant evolution, it is important that research into the ecology of the species housed there continues to approach the various themes with fresh eyes, and to develop new tools to better understand the various components inherent in animal-human proximity and seek to innovate for the well-being of zoo animals.

Supplementary Information

The initial protocol and data collection was carried out not only for gorillas, but also for a group of Geladas (*Theropithecus gelada*) also housed at La Vallée des Singes. The aim of adding this second species was to add a further component to the visitor effect: knowledge and popularity of the species. Indeed, Geladas are a fascinating and under-studied species, but above all, very little known by the public. Moreover, the location of this second territory is on the same path as the one leading to zone V2 described earlier, so it could have been very interesting to assess the attractiveness and potential visitor effect of the species in question, depending on its popularity. However, as the extraction and processing of the raw data was extremely time-consuming, it would have taken a few more months to be able to include this data in the analysis. This highlighted one of the main limitations of the present protocol: the position of individuals was recorded on paper maps, which then had to be digitized for processing in QGIS. One solution, which should be considered before replicating this protocol, would have been to collect the data using a digital tablet directly embedded in QGIS, to gain in positioning accuracy and time for reporting all the data.

Acknowledgements

I would like to thank all the people who contributed to making this thesis possible and helped me to write it.

First of all, I would like to thank my promoter, Mr. T. Hance, professor at UCLouvain, who agreed to follow me for this project and helped me to write and structure this thesis.

I would also like to thank Mr. C. Montedoro, PhD student at UCLouvain, who agreed to supervise me for this work, for his availability and his judicious advice to fuel my reflection.

I would like to express my gratitude to Mr J.P. Guéry, director of La Vallée des Singes, for his warm welcome and for allowing me to carry out my data collection independently in the park.

I'd also like to thank the BOE Master's Commission team for letting me work on a dissertation that I designed myself.

Thanks also to Mr. Alain Guillet of SMCS for his help and advice in constructing the protocol and building my data analysis models.

Finally, I'd like to thank my family and friends for your support and trust throughout my somewhat atypical career. Thank you to my Constance for putting up with my long evenings of work and for being there for me every day.

References

- Akers, J.S., Schildkraut, D.S., 1985. Regurgitation / reingestion and coprophagy in captive gorillas. *Zoo Biol.* 4, 99–109.
- Altman, J. D. (1998). *Animal Activity and Visitor Learning at the Zoo*. *Anthrozoös*, 11(1), 12–21. doi:10.1080/08927936.1998.11425083
- Anderson, Ursula S.; Benne, Marcie; Bloomsmith, Mollie A.; Maple, Terry L. (2002). *Retreat Space and Human Visitor Density Moderate Undesirable Behavior in Petting Zoo Animals*. *Journal of Applied Animal Welfare Science*, 5(2), 125–137. doi:10.1207/S15327604JAWS0502_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. *Environment and Behavior*, 35(6), 826–841. <https://doi.org/10.1177/0013916503254746>
- Besag, J. E. (1977). Comments on Ripley's paper: Royal Statistical Society. *Journal*, 39, 193–195.
- Blaney, E. C., & Walls, D. L. (2004). The influence of a camouflage net barrier on the behaviour, welfare and public perceptions of zoo-housed gorillas. *Animal Welfare*, 13(2), 111–118.
- Bonnie Kristin E., Mabel Y.L. Ang, Stephen R. Ross, Effects of crowd size on exhibit use by and behavior of chimpanzees (Pan troglodytes) and Western lowland gorillas (Gorilla gorilla) at a zoo, *Applied Animal Behaviour Science*, Volume 178, 2016, Pages 102–110, ISSN 0168 1591, <https://doi.org/10.1016/j.applanim.2016.03.003>.
- 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. In *American Journal of Primatology* (Vol. 84, Issue 10). Wiley. <https://doi.org/10.1002/ajp.23386>
- Carr, N. (2016). *An analysis of zoo visitors' favourite and least favourite animals*. *Tourism Management Perspectives*, 20, 70–76. doi:10.1016/j.tmp.2016.07.006
- Carter, Marcus; Webber, Sarah; Sherwen, Sally (2015). [ACM Press the 12th International Conference - Iskandar, Malaysia (2015.11.16-2015.11.19)] *Proceedings of the 12th International Conference on Advances in Computer Entertainment Technology - ACE '15 - Naturalism and ACI.* , (), 1–5. doi:10.1145/2832932.2837011
- Carrasco, L; Colell, M; Calvo, M; Abelló, MT; Velasco, M; Posada, S Benefits of training/playing therapy in a group of captive lowland gorillas (Gorilla gorilla gorilla) : *Animal Welfare*, Volume 18, Number 1, February 2009, pp. 9–19(11)
- Chamove, A. S., Hosey, G. R., & Schaezel, P. (1988). *Visitors excite primates in zoos*. *Zoo Biology*, 7(4), 359–369. doi: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: 445–453. <http://dx.doi.org/10.2307/1931034>.
- Clarke, A.S., Juno, C.J., Maple, T.L., 1982. Behavioral effects of a change in the physical environment: a pilot study of captive chimpanzees. *Zoo Biol.* 1, 371–380.
- Clark Fay E. (2011). *Great ape cognition and captive care: Can cognitive challenges enhance well-being?* , 135(1-2), 1–12. doi:10.1016/j.applanim.2011.10.010
- 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: 558–577. <http://dx.doi.org/10.1034/j.1600-0587.2002.250506.x>.
- Davey, G. (2006). *Relationships between exhibit naturalism, animal visibility and visitor interest in a Chinese Zoo*. *Applied Animal Behaviour Science*, 96(1-2), 93–102. doi:10.1016/j.applanim.2005.04.018
- de Freitas Alves, G., & de Santana, D. G. (2021). Why do traditional dispersion indices used for analysis of spatial distribution of plants tend to become obsolete? In *Population Ecology* (Vol. 64, Issue 2, pp. 80–92). Wiley. <https://doi.org/10.1002/1438-390x.12105>
- Forthman Quick, D.L., 1984. An integrative approach to environmental engineering in zoos. *Zoo Biol.* 3, 65–77.
- Glatston, A., Geilvoet-Soeteman, E., Hora-Pecek, E., & van Hooff, J. (1984). The influence of the zoo environment on social behavior of groups of cotton-topped tamarins (*Saguinus oedipus*). *Zoo Biology*, 3, 241–253.
- Godinez, A. M., Fernandez, E. J., & Morrissey, K. (2013). *Visitor Behaviors and Perceptions of Jaguar Activities*. *Anthrozoös*, 26(4), 613–619. doi:10.2752/175303713x13795775535850
- Gold Kenneth C.; Maple Terry L. (1994). Personality assessment in the gorilla and its utility as a management tool. , 13(5), 509–522. doi:10.1002/zoo.1430130513
- Hashmi, Anita and Sullivan, Matthew (2020) The visitor effect in zoo-housed apes: the variable effect on behaviour of visitor number and noise. *Journal of Zoo and Aquarium Research*, 8 (4). pp. 268–282. ISSN 2214-7594 <https://doi.org/10.19227/izar.v8i4.523>
- Huffman Alejandro, J., M. A., & Bercovitch, F. B. (2022). Costs and benefits of living in a vegetated, compared with non-vegetated, enclosure in male Japanese macaques (*Macaca fuscata*). *ZooBiology*, 41(2), 97–107. Wiley. <https://doi.org/10.1002/zoo.21657>

- Hosey, G., & Druck, P. (1987). The influence of zoo visitors on the behavior of captive primates. *Applied Animal Behavior Science*, 18, 19-29
- Hosey Geoffrey R. (2005). *How does the zoo environment affect the behaviour of captive primates?*, 90(2), 107-129. doi:10.1016/j.applanim.2004.08.015
- Kint V., Meirvenne M. van, Nachergale L., Geudens G., Lust N. (2003). Spatial methods for quantifying forest stand development: a comparison between nearest neighbor indices and variogram analysis. *Forest Science* 49: 36-49.
- 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*. *Biophysical Journal*, 97(4), 1095-1103. doi: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, 292-306. doi: 10.1002/zoo.20226
- Law, R., Illian, J., Burslem, D. F. R. P., Gratzner, G., Gunatilleke, C. V. S., & Gunatilleke, I. A. U. N. (2009). *Ecological information from spatial patterns of plants: insights from point process theory*. *Journal of Ecology*, 97(4), 616-628. doi:10.1111/j.1365-2745.2009.01510.x
- Le Flohic, G., 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>
- Létang B, Mulot B, Alerte V, Bionda T, Britton L, ter Meulen T, Szańthó J, Guéry J-Pascal, Sueur C, Social proximities of developing gorilla males (*Gorilla gorilla gorilla*) in European zoos: the consequences of castration and social composition, *Applied Animal Behaviour Science* (2020)
- Lewis, R. N., Chang, Y., 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 Biology*, 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*. *Canadian Journal of Forest Research*, 38(12), 3112-3119. doi:10.1139/x08-143
- Mace GEORGINA M. (1988). *The genetic and demographic status of the Western lowland gorilla (Gorilla g. gorilla) in captivity*. , 216(4), 629-654. doi:10.1111/j.1469-7998.1988.tb02462.x
- Maple, T.L., Finlay, T.W., 1989. Applied primatology in the modern zoo. *Zoo Biol.* 1 (Suppl.), 101-116. (Lewis et al. 2020)
- 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. doi:10.2752/089279304786991792
- Mittermeier Russell A., Anthony B. Rylands, and Don E. Wilson (eds.). 2013. *Handbook of the Mammals of the World: 3. Primates*. Lynx Ediciones, Barcelona, Spain, 953 pp. ISBN: 978-84- 96553-89-7
- Moss, A., & Esson, M. (2010). *Visitor interest in zoo animals and the implications for collection planning and zoo education programmes*. *Zoo Biology*, 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. doi: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 Biology*, 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*. *American Journal of Primatology*, 56(4), 193-206. <https://doi.org/10.1002/ajp.1074>
- Philpot, P. (1996). *Visitor viewing behaviour in the Gaherty reptile breeding Centre, Jersey wildlife preservation trust: a preliminary study*. *Dodo J. Jersey Wildlife Preserv. Trust* 32, 193-202.
- Ripley, B. D. (1976). *The second-order analysis of stationary point processes*. *Journal of Applied Probability*, 13(02), 255-266. doi:10.2307/3212829
- Ripley, B. D. (1977). *Modelling Spatial Patterns*. *Journal of the Royal Statistical Society: Series B (Methodological)*, 39(2), 172-192. doi:10.1111/j.2517-6161.1977.tb01615.x
- Rooney, Matthew B.; Sleeman, Jonathan (1998). *Effects of Selected Behavioral Enrichment Devices on Behavior of Western Lowland Gorillas (Gorilla gorilla gorilla)*. *Journal of Applied Animal Welfare Science*, 1(4), 339-351. doi:10.1207/s15327604jaws0104_2
- Rose, P., & Croft, D. (2015). *The potential of Social Network Analysis as a tool for the management of zoo animals*. *Animal Welfare*, 24(2), 123-138. doi:10.7120/09627286.24.2.123
- Rose, P. E., Scales, J. S., & Breerton, 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*. *Frontiers in Veterinary Science*, 7. doi: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)*. *Applied Animal Behaviour Science*, 96(1-2), 143-152. <https://doi.org/10.1016/j.applanim.2005.06.005>
- Simons, Noah D.; Wagner, Ronald S.; Lorenz, Joseph G. (2013). *Genetic diversity of North American captive-born gorillas (Gorilla gorilla gorilla)*. *Ecology and Evolution*, 3(1), 80-88. doi:10.1002/ece3.422
- Strindberg, S., Maisels, F. et al. (2018). *In prep. Guns, germs and trees: key factors influencing the status of gorillas and chimpanzees in Western Equatorial Africa*. DOI: 10.1126/sciadv.aar2964
- Stoinski, T.S., Hoff, M.P. & Maple, T.L. (2001). *Habitat Use and Structural Preferences of Captive Western Lowland Gorillas (Gorilla gorilla gorilla): Effects of Environmental and Social Variables*. *International Journal of Primatology* 22, 431-447. <https://doi.org/10.1023/A:1010707712728>
- Stoinski T.S.; M.P. Hoff; T.L. Maple (2003). *Proximity patterns of female western lowland gorillas (Gorilla gorilla gorilla) during the six months after parturition*. , 61(2), 61- 72. doi:10.1002/ajp.10110
- Stoinski T.S.; K.E. Lukas; C.W. Kuhar; T.L. Maple (2004). *Factors influencing the formation and maintenance of all-male gorilla groups in captivity*. , 23(3), 189-203. doi:10.1002/zoo.20005
- Turner, R. Point patterns of forest fire locations. *Environ Ecol Stat* 16, 197-223 (2009). <https://doi.org/10.1007/s10651-007-0085-1>
- Thompson, V. (1976). *Observation of the great apes in a naturalistic zoo environment*. Chicago: Lin-coln Park Zoo. Unpublished manuscript. *welfare of zoo-housed gorillas*. , 93(1-2), 13-17. doi:10.1016/j.applanim.2005.06.019

Wade, A. D., Wang, L.-P., & Huggins, D. J. (2018). *Assimilating Radial Distribution Functions To Build Water Models with Improved Structural Properties*. *Journal of Chemical Information and Modeling*. doi: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*. *Applied Animal Behaviour Science*, 93(1-2), 13-17. <https://doi.org/10.1016/j.applanim.2005.06.019>

Williams, E., Carter, A., J., Fontani, S., Walsh, N.D., Armstrong, S., Hickman, S., Vaglio, S., & Ward, D.J. (2022). The impact of COVID-19 Zoo Closures on Behavioural and Physiological Parameters of Welfare in Primates. In *Animals* (Vol. 12, Issue 13, p. 1622). MDPI AG. <https://doi.org.10.3390/ani12131622>

Zbigniew H. Stachurski, *Fundamentals of Amorphous Solids: Structure and Properties*, John Wiley & Sons (2015) Geometry of Sphere Packings. p.47

List of abbreviations

P1/P2 - Proximal zones 1 and 2

Dist - Distal Zone

V1 - Visitor Zone 1

V2 - Visitor zone 2

ItP1/ItP2 - Exposure Tolerance Index in zone P1/P2

Riv1 - Retreat index when visitors are present in V1

Riv2 - Retreat index when visitors are present in V2

RiV1V2 - Retreat index when visitors are present in V1 and V2 simultaneously

Appendix

Table 4. Factors Loadings for the Gorilla Behavioral Index as described by Gold & Maple (1994)

| Extroverted | Dominant | Fearfull | Understanding |
|-------------|-----------------|----------------|-----------------|
| Sociable + | Aggressive + | Fearfull + | Understanding + |
| Playful + | Effective + | Appregensive + | Protective + |
| Active + | Irritable + | Insecure + | Permissible + |
| Popular + | Strong + | Tense + | Equable + |
| Curious + | Opportunistic + | Eccentric + | Motherly + |
| Solitary - | Excitable + | Confident - | |
| Slow - | | | |

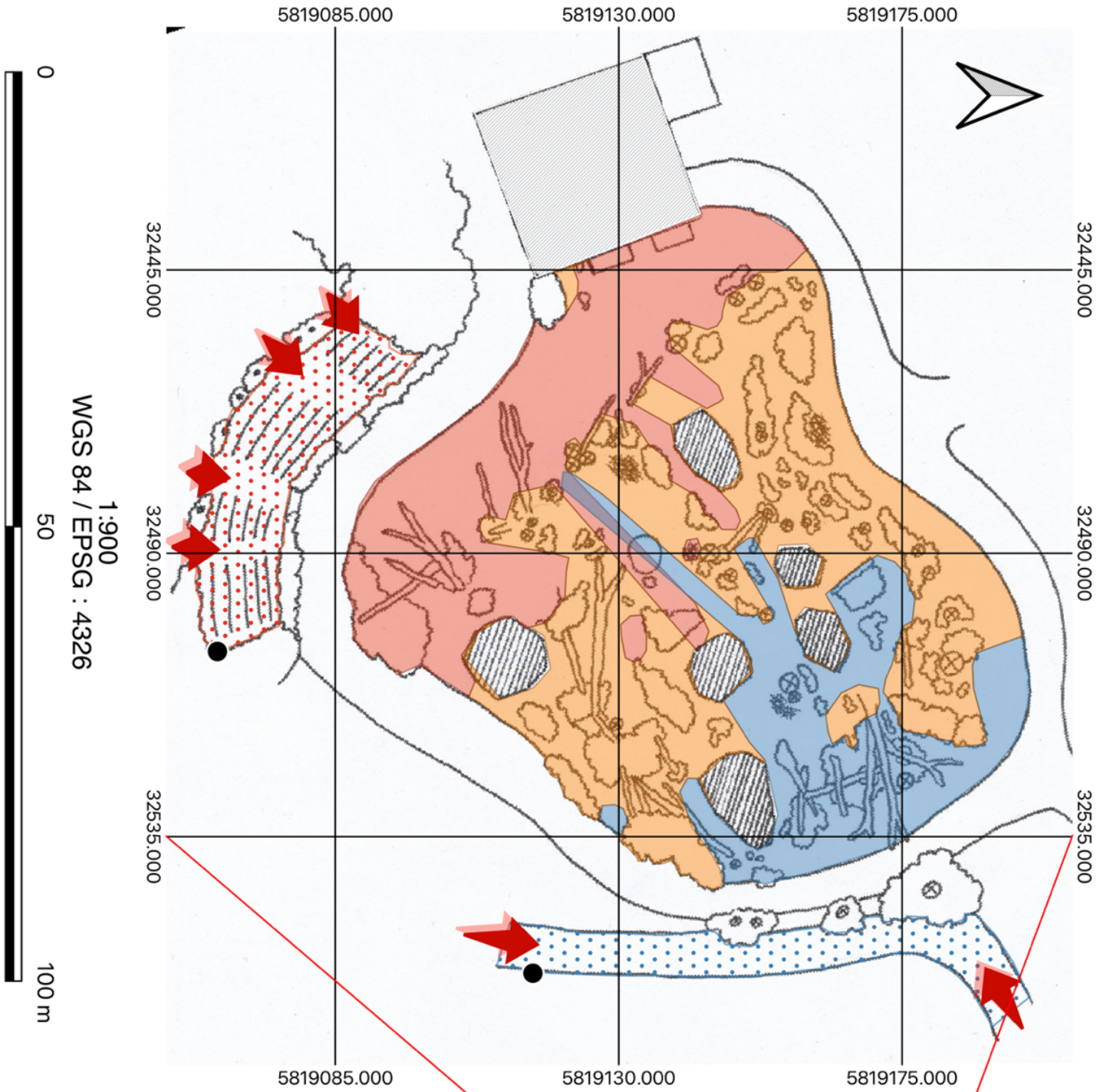
+ = positive loadings ; - = négative loadings.



Figure 13. Positioning and overview of the Camera device used to count visitors in zone V2.



Figure 14. Positioning and overview of the Camera device used to count visitors in zone V1.



1:900
WGS 84 / EPSG : 4326



- Trees
- Night building
- Possible visitor traffic directions
- camera trap
- Proximal zone 1 (P1)
- Proximal zone 2 (P2)
- Distal zone (Dis)
- Visitor zone 1 (V1)
- Visitor zone 2 (V2)
- Preserved spaces

