

The Behavioral Sequences of Mountain Gorillas Under Tourism Pressure – Insights for Tourism Sustainability

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Abstract: Recent evidence highlights behavioral changes in mountain gorillas being watched by tourists, especially when the recommended 7-m distance is breached. Notably, significant effects were observed at shorter distances, particularly 3 m, where tourists predominantly spend their time during the designated tourist hour. Existing studies, however, have focused primarily on “how much” behavior has changed but not on “how” behavior has changed. This study focuses on behavioral flexibility (transition quality, i.e. shift of one behavior to another) and diversity (transition frequency) to provide insights into how gorilla behavior is affected by tourists. We conducted initial observations of behavior in mountain gorillas near tourists in Bwindi Impenetrable National Park, Uganda. We studied 19 behaviors in a group of 15 mountain gorillas, examining the first behavioral transition (behavior A shifts to behavior B) under various conditions: 1) before tourist arrival; 2a) during tourist visits within 3 m; 2b) during tourist visits generally beyond 3 m; 3a) during tourist visits at distances of 3–7 m; 3b) during tourist visits at distances of 7 m away; and 4) after tourist visits. We calculated transition probabilities using Ethoseq to assess flexibility, and for each condition, we used a Generalized linear mixed model (GLMM) to compare the number of behavioral transitions to evaluate the gorillas’ behavioral diversity as a function of condition and age-sex class. Our study revealed that behaviors such as scratching, affiliation, and human-directed actions displayed significant associations during tourist proximity. The organization of these behaviors depended on the gorillas’ age-sex class. Gorillas showed lower behavioral flexibility (represented by less significant transitions) and lower diversity (represented by the lower mean number of transitions) during tourist visits. During the tourist visit, diversity and flexibility were higher at close distances to tourists. These results contribute to the growing body of evidence highlighting the impact of tourists on the animals’ behavior in their natural habitats. To protect gorilla welfare, gorilla tourism requires better control and restraint of the tourists’ activities. Measures may include stricter enforcement of the 7-m safety-distance rules and the adoption of assertive messaging techniques upon permit acquisition. The implementation of more restrictive tourist management practices during viewing experiences is also essential.

Introduction

Behavior is selected to provide individuals with ways to cope with the environment and other animals, both conspecifics and other species. Individuals show specific sequences or patterns of more or less predictable behavioral responses that may show high or low behavioral diversity (typical patterns of behavior considered to be part of the species’ natural repertoire) (Brandão *et al.* 2019; Miller *et al.* 2021). The variation of these behavioral sequences can enhance an individual’s ability to adapt to changes in the environment, with fundamental ecological consequences (George *et al.* 2015; Caspi *et al.* 2022) while providing clues about the individual’s welfare status. Variations in behavioral structures include examples such as the relation between anti-predator behavior

and predation (Steiner and van Buskirk, 2008), parental and offspring behavior (Fresneau and Muller 2019; Lucass *et al.* 2016), shifts in diet and opportunistic behavior (Nowak and Lee 2013) or variations in animal responses to anthropogenic activities (van Buskirk 2012; Caspi *et al.* 2022). The mechanisms underlying such variations in responses may help us to predict how animals respond to environmental changes and compare species’ resilience. Accordingly, incorporating behavioral changes into conservation plans, including flexibility and diversity, becomes crucial in addition to endeavors to preserve genetic diversity and ecosystem health (Cordero-Rivera, 2017). Here, we define behavioral flexibility as transitions from and to different behavior categories and behavioral diversity as the number of behavioral transitions. While some suggest that, in general, plastic

responses are not enough to cope with human disturbance (e.g., van Baaren and Candolin 2018) but many reports on primate resilience offer a more optimistic view. Vervet monkeys, for example, present different responses when sharing human landscapes (i.e., in sentinel behavior and ranging patterns), which depend on the habitat type, and which allows them to survive in areas they share with humans (Chapman *et al.* 2016; Thatcher *et al.* 2019). For primates that experience more constant and direct contact with humans, those subject to tourism, for example, studies have documented detrimental effects (Bateman and Fleming 2017; Geffroy *et al.* 2015). They include compromised reproductive performance (*Cebuella pygmaea*: de la Torre *et al.* 2014), increased infant mortality (*Macaca thibetana*: Berman *et al.* 2014; *Alouatta pigra*: Grossberg *et al.* 2003), and declines in population size (*Propithecus edwardsi*: Wright *et al.* 2014). On an immediate level, different primates seem to have developed similar coping mechanisms to reduce stress such as social buffering (*Macaca fascicularis*: Marty *et al.* 2019; *Macaca sylvanus*: Majolo *et al.* 2013; Marechal *et al.*, 2016; *Gorilla beringei beringei*: Mabano, 2013; Steklis *et al.* 2014; Costa *et al.* 2023a, 2023b), and increased aggression towards people (*Gorilla gorilla gorilla*: Klailova *et al.* 2010; *G. beringei beringei* Costa *et al.* 2023b). The value of immediate stress responses is that they provide individuals with the awareness and responses necessary to cope with challenges via activation of the hypothalamic-pituitary-adrenal (HPA) axis, resulting in hormonal changes turning off non-essential mechanisms and redirecting energy to fast counteract stress factors (Monaghan and Haussmann 2015; Boonstra *et al.* 2013; Reser 2016). In mountain gorillas, coping mechanisms such as social buffering were shown to be pronounced during periods of extreme proximity to large groups of tourists (Costa *et al.* 2023a, 2023b), resulting from the tourists' clear disregard for the recommended 7-m distance guideline proposed to safeguard the gorillas' welfare and health (Macfie and Williamson 2010; Weber *et al.* 2020). Gorilla tourism is nonetheless a vital conservation tool for this species, which has no potential for *ex situ* conservation measures. It provides a critical umbrella and flagship effect for the region. As such, assessment of the nature and level of disturbance experienced by the ambassador groups of mountain gorillas is vital for the development of measures that minimize stress, contributing to their well-being and as such, more sustainable gorilla tourism. In captivity, negative stress indicators such as stereotypic behavior and self-harming are commonly used to assess their well being, but the absence of these indicators in the wild does not mean that they are not under similar stress.

Here, we use probabilistic and statistical analysis of behavioral sequences to detect changes in the behavioral flexibility and diversity of individuals in a group of mountain gorillas in Bwindi, Uganda, to (1) explore the significant (i.e., above-chance) behavioral transitions related to social behaviors, stress-indicative behaviors, and interactions, following up recent claims that these behaviors

are potential coping mechanisms that they adopt in dealing with tourist presence and close proximity (Costa *et al.* 2023a, 2023b), and 2) to explore differences in behavioral diversity of such sequences across conditions. Behavioral sequences measured by different analytic tools have been used in assessments of both human and non-human animals to assess complexity in personality traits (Brandão *et al.* 2019), the behavioral repertoire of species (Banerjee *et al.* 2021), reaction to disturbance (Kembro *et al.* 2009), an individuals' daily routines (Lunardi and Ferreira 2012), and the relation between behavioral complexity and health (Alados *et al.* 1996; MacIntosh *et al.* 2011; Miller *et al.* 2021). Asher *et al.* (2009) reviewed the potential analytical tools to measure such behavioral structures. More recent studies have shown an inverse relationship between behavioral diversity and physiological stress markers and stereotypic behavior (Miller *et al.* 2021), lending support to behavioral diversity as an indicator of animal welfare.

Despite the emergence of new analytical tools, the complexity of behavior is most often reduced to the analysis of frequencies or percentages of time the individuals spend performing different types of behavior, with no information about how such behaviors are temporally structured (Kembro *et al.* 2009) or the range and variety of behaviors exhibited by an individual within its species-typical repertoire. The examination of how behaviors transition from one to another provides a means to assess qualitative differences in the structure of behavior. Such tools are more sensitive to detecting behavioral outcomes of acute stress compared to frequency-based measures, and are independent of the amount of data analyzed (Kembro *et al.* 2009; MacIntosh *et al.* 2011, 2014; Brandão *et al.* 2019; Miller *et al.* 2021). For instance, a decrease in the complexity of the organization of behavioral sequences was directly associated with increased stress due to parasitic infection (Alados *et al.* 1996) and painful procedures (Kembro *et al.* 2009). As such, studies on animal welfare, conservation, and wildlife management can benefit from the analysis of behavioral patterns as early indicators of proximate stressors (MacIntosh 2014; Deakin *et al.* 2019).

Previous studies have shown the disruptive effect that proximity of tourists has on the behavior of mountain gorillas. We tested the following hypotheses: 1) mountain gorillas will show lower behavioral flexibility (less above-chance transitions) and diversity (lower frequency of transitions per observation) during tourist visits compared to periods without tourists (*before* and *after* the tourist-visit hour), and particularly during close proximity to tourists (*during* <3 m) compared to greater distances from tourists (*during* >3 m) during the visit hour (with potential differences between distances of *during* 3–7 m and *during* >7 m); 2) transitions from or to social and stress-related behaviors (pro-social behaviors and self-scratching) will be more common *during* <3 m contact with tourists; and 3) sex-age class differences will show different trends in the quantity and quality of the observed behavioral flexibility and behavioral diversity.

Methods

Study subjects and location

The study subjects were habituated mountain gorillas of the Rushegura group in the Buhoma sector of the Bwindi Impenetrable National Park, hereafter referred to as Bwindi, in southwestern Uganda. Age/sex classifications for mountain gorillas followed Williamson and Gerald-Steklis (2002): adult male (silverback) >12 years, (blackback) >8–12 years, adult female >8 years, subadult >6–8 years, juvenile >3.5–6 years, and infant > 0–3.5 years. Fifteen focal subjects were selected by age-sex class: one silverback, two blackback males, one sub-adult male, seven adult females, and four infants (all independent from the mother and showing individual behaviors towards tourists). The Rushegura group has been visited by tourists daily since the late 1990s and was among the initial gorilla groups to undergo habituation in the park. All but two members (adult females Buzinza and Kibande), were born in the group habituated to tourists. To learn more about the stages of habituation and the initial groups habituated for tourism in Bwindi, please consult Kabano *et al.* (2014).

Data collection

One researcher (RC) followed the gorillas for 4 hours per day, happening sometime between 07:20 and 16:30 depending on the time the gorillas were found in the morning. Two months of pilot data collection (September–October 2017) were conducted to validate the methods before data collection was started. Formal data collection occurred 5–6 days per week over 9 months (between December 2017 and February 2019). Behavioral data collected on gorilla encounters with tourist groups were divided into two periods: a) tourists present (tourist group visit) and b) tourists absent (before and after the arrival of the tourist group). When the tourists were present, data were also collected on the distance between gorillas and the closest tourist in the tourist group, providing a proportion of time spent in each distance category per focal animal: a) <3 m, b) 3–7 m, and c) >7 m. Distance estimation was practiced before data collection using a measuring tape, and success was considered satisfactory, with 19 out of 20 sessions being successful in estimating the distance categories.

We collected data on 19 behavioral categories using 10-min continuous recording sessions (Martin and Bateson 2007) (Table S1). If the focal subject was not visible for more than 2 min, then observations were terminated, and the focal session was excluded from the analyses. The order of the focal subjects was determined each day by selecting individuals which had fewer sessions recorded during a specific period (before, during, and after tourist visits) in order to balance data collection between categories and individuals, following Thompson and Cords (2018). Each individual was equally monitored to ensure a comparable amount of focal time during each condition (refer to supplementary

material Table S2). Additional details on the data collection protocol can be referenced in Costa *et al.* (2023b).

In all, RC obtained 577 hours of behavioral data, including 182.6 hours when tourists were present. Tourist groups (using the nearest tourist of each group as a reference) spent 59.20%, 25.63%, and 15.17% of the time at <3 m, 3–7 m, and >7 m, respectively, away from the focal gorilla. To better balance the amount of data across categories, we first combined groups at 3–7 m and >7 m into a single category, corresponding to a new category of >3 m, which could be compared to the category <3 m. We then compared the categories of 3–7 m and >7 m which can be compared with each other because they have similar amounts of data. Further quantitative data on tourist group size, the amount of data collected per individual gorilla, and the distribution of observations during the day can be found in Costa *et al.* (2023a, 2023b).

Flexibility: Probabilistic analysis of behavioral sequences

To understand the immediate behavioral responses of gorillas to the presence and proximity of tourists, we compared the gorillas' first-order transition of behaviors (i.e. first shift or change from one type of behavior to another [A followed by B]; the second-order transition would be the second change of behavior in that sequence [A followed by B and B followed by C]) across the following conditions of tourist presence/absence and proximity to gorillas: 1) before tourist arrival; 2) during the tourist visit, when tourists are within 3 m of the gorillas; 3) during tourist visit, when tourists are more than 3 m away from the gorillas; 4) during the tourist visit, when tourists are between 3 and 7 m from the gorillas; 5) during the tourist visit, when tourists are more than 7 m away from the gorillas; and 6) after the tourist visit. We created transition matrices for each condition, for each age-sex class (adult females, adult males, and infants), and included all recorded behaviors (see Ethogram in Table 1). A transition matrix has the preceding behavior in a row and subsequent behaviors as columns, and each input to a matrix cell is a transition that happens between the behavior of the preceding (row) and subsequent (column). We considered each focal session as a behavioral sequence (refer to supplementary material Table S1).

The matrices were analyzed using EthoSeq (Japyassú *et al.* 2006), a program extracting the sequences provided by the matrices, using Mathematical Graph Theory. Benefits for the analysis of the probability of transition between behaviors include temporal-scale independent, detailed information on *how* animals behave in each condition instead of *how much* behavior they perform in each condition, the ability to analyze diverse features, such as detection of behavioral differences between treatments, measurement of the diversity of a behavioral repertoire, comparison of the behavioral plasticity among different species and the phylogenetic analysis of behavior (Japyassú *et al.* 2006). Ethoseq-directed trees (hierarchical diagrams showing the percentage probability for each transition) reveal the relative

probabilities of occurrence (e.g., behavior B has a percentage of chance happening after behavior A). EthoSeq calculates the expected probability of each behavioral transition based on the observed probabilities of the two behaviors involved in the transition, as well as the null distribution of expected probabilities generated by the Brown chi-square test (1974). If the actual probability of the transition is higher than the expected probability, the transition is considered to be significant by identifying transitions above- and below-chance transitions to find specific behavioral structures that are driving the differences between conditions. We chose a significance level of 99% and decided to keep

the above-chance significant transitions only. This approach helps to identify transitions that are more frequent than what would be expected by chance alone and are therefore likely to be biologically meaningful.

Given that the accuracy of the estimation of probabilities weakens to chance levels relatively quickly following the first transition level (Thatcher and Insel 2021) and because second transitions entail a conditioned probability (i.e., probability of X given Y), we chose to analyze the first transition for each behavior only. In the discussion section, we focus only on behaviors of interest according to this study's hypotheses (affiliation, scratching and self-directed

Table 1. Behavioral categories used in the data analysis. Adapted from the GBAG Gorilla Ethogram Compilation of Ogden *et al.* (1991).

Categories	Definition	
Affiliation	Provider	Pro-social behaviors between individuals such as allogrooming, greeting, muzzle-muzzle, kissing, touching, embracing, and resting in physical contact.
	Receiver	
Play	Exaggerated, rambling, and apparently no purposeful behavior between at least two individuals. May include direct contact between parties by wrestling, tickling, standing or climbing upon, slapping, poking, kicking, carrying, ambushing, pushing, mauling, sparring, dangling, piggyback ride, and mouthing without serious biting. Play may be confused with aggression, which should be differentiated by the play face expression (open mouth exposing teeth, but lips relaxed at the edges), chuckling, or a throaty grumbling. It also may happen without direct contact, by chasing, throwing, or slapping objects (including water), chest-beating, arm shaking or turning circles around, and chasing the other. It also includes soliciting play behavior (runaway, swagger, chest beat) to elicit play from another. Includes solitary play.	
Agonism	Provider	Includes supplanting, stare (visual gaze), rigid quadrupedal stance or walk, head divert, object or ground slap, leg kick, chest beat, open-mouth threat, pursed-mouth, threat display, bluff charge, rush charge, attack, bite, slap, and drag.
	Receiver	
Submission	Provider	Includes turning away directly from another, running, avoiding, hiding, crouching/crawling (making the body look smaller), and presenting (genital presenting with no sexual intention or presenting arm or other body part).
	Receiver	
Mating	Genital inspection, mount attempt, mount, mount and thrust, and copulation.	
Mother-directed	Affiliative behaviors directed to mothers, transport, play, and breastfeeding.	
Infant-directed	Affiliative and agonistic behaviors directed to infants, transport, play and breastfeeding.	
Move	Spatial movement from one point to another, varying the speed and method, without any other activity (social or individual). It may include walking (bipedal or quadruple), running, sliding, climbing, jumping, and swinging. It excludes solitary play and locomotion during social interactions.	
Feeding	Foraging, processing, and ingesting food.	
Inactivity	Absence of behavior (for 5 seconds or more) or eliminating behaviors such as defecating or urinating. It may include also rest and sleep, when the individual is not in contact with another group member. The individual may be lying down (ventral, dorsal or laterally), seated or squatting.	
Scratch	Repetitive up and down movement using fingertips to scrape a precise area of the body.	
Self-directed	Cleaning of own fur, using hands or mouth, for more than 5 seconds; auto-inspection (close visual or olfactory examination of own body area). It excludes licking fingers during feeding, regurgitation, or re-ingestion.	
Vigilance	Visual attention, gazing, or monitoring directed to focus areas, conspecifics, or visitors while in quadrupedal stance; interruption of the previous behavior to focus on a specific individual or area, while still seated or standing.	
Human-directed behavior	Neutral	Actions involving physical touch to visitors (for example, while moving to pass by tourists, or by direct approach to visitors), and indirect interactions with visitors by extending arms, clapping hands, arm shake, and chest pats in their direction.
	Agonism	Actions hostile to humans, such as an agonistic display with chest-beating, growling, roaring, open-mouth threats, running towards or sideways past the human, but not hitting them.
	Avoidance	Avoiding or fleeing from humans.
Out of sight of the observer		

behaviors, and interactions with tourists and park staff). To test our hypothesis that gorillas may decrease the frequency of behavioral transitions during tourist presence (in particular at short distances to tourists) and shift to stress-related behavior more often during the same periods, we compared how these behaviors of interest changed across conditions by visually inspecting the outcome trees and comparing the probabilities associated with each pair of transitions.

Diversity: Statistical analysis of the variation of transitions across conditions

We also calculated the number of transitions per session for each age-sex class to provide a visualization of the mean variation of transitions in each condition and Class (Adult female, Adult male, and Infant). To compare the number of behavioral transitions as a function of *Class* and *Condition*, three generalized linear mixed models (GLMM) were used to predict the count of behavioral observations (independent variable) as a function of the *Period* (*before*, *during*, and *after*) and *Class* for model 1; of *Distance 1* and *Class* (*during <3 m* and *during >3 m*) for model 2; and of *Distance 2* (*during 3–7 m* and *during >7 m*) and *Class* for model 3. In both models, the individual's identity (ID) was used as a random effect. We chose a negative binomial distribution as the family argument in the model over the Poisson distribution based on the lowest AIC value. The AIC (Akaike Information Criterion) quantifies the trade-off between a model's goodness of fit and complexity, with lower AIC values indicating a more suitable model. Diagnostic tests were performed and showed that the model assumptions, such as the absence of overdispersion and heteroscedasticity, were met. To check for multicollinearity, we calculated the variance of the model matrix using the "var" function, providing the variance of each predictor variable which were all below 1. We used R version 4.2.3 and packages *ggplot2* (Wickham 2016) and *glmmTMB* (Brooks *et al.* 2017) for these analyses.

Results

Flexibility: Significance of behavioral transitions identified by EthoSeq

The number of significant transitions found ranged between 12 and 21 *during <3 m* and between 11 and 18 *during >3 m*, while the number of significant transitions ranged between 9 and 27 *before* the tourists' arrival and between 18 and 26 *after* the tourists' departure (Table 2). Details on the transition probabilities made by age-sex class and by the condition can be found in the supplementary material Table S2. Females appeared to show transitions to feeding behavior and inactivity across conditions but, overall, showed a greater number of transitions in the absence of tourists. Males followed the same pattern with more diverse transitions in the absence of tourists but they mainly transitioned to moving *before* tourists, to inactivity *during <3 m*, to scratching *during >3 m* to tourists, and to inactivity and feeding *after* the tourists' departure. Males also showed

the least variety of transition types *during 3–7 m* and *during >7 m*. Infants, on the other hand, showed the least variety of transition types *before* tourists' arrival (they focused on mother-directed behaviors) but a great variety *after* tourist visiting hours. Nonetheless, at this time, their most significant transition was to inactivity. We should note that transitions to scratching behavior were more common in the *during <3 m* condition, and transitions to human agonism and human-fear behaviors only appeared in the *during <3 m* condition. Overall, the most common significant transition across all conditions was inactivity, followed by transitions to feeding. These are also the most frequent behaviors in the mountain gorillas' daily activity budgets.

Scratching was the most common transition for males *during >3 m* and *during 3–7 m*. In turn, transitions from scratching to self-directed and inactivity were above-chance in all conditions. This pattern was also observed in females, except in *during <3 m* and *during 3–7 m*, in which they mainly became inactive after scratching. Likewise, self-directed behavior consistently induced scratching and inactivity across all conditions in females (except for *during >7 m*) and likewise *during* and *after* tourists for males. For females, it also promoted inactivity from the moment of the tourists' arrival, and vigilance and human avoidance and inactivity *after* the tourists' departure; for males' vigilance was triggered following self-directed behavior *during <3 m*. Like males, scratching was a common transition during tourist visits for infants, but unlike adult males, transitioning to scratching was more pronounced *during <3 m*. Similar to adults, scratching induced self-directed behavior *during <3 m* and *after* the tourists' departure while self-directed also induced scratching *during <3 m*.

Transitioning to Affiliation provider was also a very common behavior in adult males *during >3 m* tourists' visits, it is noticeable that affiliation induced play and vigilance *before* tourists but agonism *after* tourists' visits. As an anticipatory behavior, the affiliation receiver seemed to promote affiliation provider *before* the tourists' arrival and to promote play and affiliation provider *during >3 m* and *during >7 m*, but there were no significant transitions from any type of affiliative behavior *during <3 m* contacts. Affiliation was also associated with other forms of social behavior in females in the absence of tourists (play, affiliation, agonism, and submission). Affiliation provider was also a frequent post-behavior transition in infants *during* the tourists' visit, disregarding the distance to tourists. In infants, affiliation provider persisted as a common transition *after* the tourists left. It was normally followed up by play behavior, while play-behavior-induced affiliation occurs across all conditions except *before* the tourists' arrival. It is important to emphasize that affiliation provider is not a common transition behavior before the arrival of the tourists.

Despite human interactions being the less frequent type of behavior when compared to inactivity and feeding, and quick in duration, it is worth describing the transitions to and from human interactions for the extent of this study.

Before the tourists' arrival, we found that vigilance preceded aggression to park staff in males; in the same period, females always became vigilant after interacting with the staff. These agonistic interactions with park staff early in the morning also seemed to set off physical interactions with staff, which in turn promoted movement in males. On top of that, agonistic interactions with both the tourists and the park staff *during* <3 m contacts promoted subsequent feeding in males. In females, agonistic interactions with the tourists and park staff *during* <3m encounters triggered mainly human-directed behavior. In the early morning, females focus on infant care after avoiding staff and, later on, *during* <3 m contacts with tourists, the females tend to move and become vigilant after avoiding tourists or get into physical contact with tourists and staff after agonistic warnings. Like mothers, following agonistic interactions with park staff *before* the tourist visit, the infants' priority was mother-directed behavior. Also, direct interactions with tourists and park staff, seem to trigger human avoidance *during* <3 m and scratching behavior. Scratching behavior was also induced by agonism to humans *during* <3 m encounters.

Diversity: Comparing the number of behavioral transitions across conditions

We found evidence of age-sex differences in the number of behavioral transitions. Adult males and Infants showed more transitions than Adult females (Fig. 1). The number of

transitions *before* was significantly higher than *during*, when comparing the periods of the presence of tourists (Table 3).

During tourist visits, gorillas showed an increase in the number of transitions at distances closer than 3 m compared to greater distances, with males displaying the most notable increase (Fig. 2). Moreover, adult females and adult males showed an increase in the number of transitions during distances greater than 7 m from tourists compared to distances of 3–7 m from tourists. In contrast, infants deviated from this pattern, exhibiting a decline in the number of behavioral transitions at distances beyond 7 m from tourists compared to distances of 3–7 m (Fig. 3).

Discussion

Human presence and behavior may drive profound changes in the gorillas' behavior but a deeper understanding of changes in more subtle behavioral patterns is crucial for the development of effective management plans (Whitehead 2010; Seiler and Robbins 2016; Costa *et al.* 2023a, 2023b). The assessment of behavior sequences can provide supplementary and more sensitive data compared to the standard behavioral analysis that disregards the structure of the activity, highlighting the diversity of responses and temporal behavioral patterns (Kembro *et al.* 2009). To our knowledge, the present study is a first attempt to explore how mountain gorillas organize their activities under tourism pressure by looking at the flexibility and diversity of their behavioral sequences. We found evidence that behaviors

Table 2. Significant transitions (STs) identified by Ethoseq, in relation to Class and Condition. The comprehensive summary of the percentage of each behavioral sequence is available in Table S2 of the supplementary material.

ADULT FEMALES	During					
	<i>Before</i>	<3 m	>3 m	3–7 m	>7 m	<i>After</i>
Prevalent transition (%)	Feeding & agonism	Inactive	Inactive	Inactive	Move	Inactive
Prevalent transition (counts of STs)	Feeding (27 STs)	Move & Inactive (21 STs)	Feeding & Inactive (18 STs)	Inactive (12 STs)	Move & Feeding (14 STs)	Feeding & Inactive (26 STs)
MALES	During					
	<i>Before</i>	<3 m	>3 m	3–7 m	>7 m	<i>After</i>
Prevalent transition (%)	Move	Inactive	Scratch	Scratch	Play	Inactive
Prevalent transition (counts of STs)	Move (24 STs)	Inactive (12 STs)	Scratch & Affiliation provider (11 STs)	Scratch (7 STs)	Play (7 STs)	Feeding & Inactive (18 STs)
INFANTS	During					
	<i>Before</i>	<3 m	>3 m	3–7 m	>7 m	<i>After</i>
Prevalent transition (%)	Mother directed	Scratch	Mother directed	Mother directed	Mother directed	Inactive
Prevalent transition (counts of STs)	Mother directed (9 STs)	Affiliation provider & Scratch (17 STs)	Affiliation provider (15 STs)	Mother directed, Feeding & Inactive (9 STs)	Mother directed & Affiliation provider (10 STs)	Affiliation provider, Submission provider & Inactive (26 STs)

Table 3. Generalized mixed-effects model fit by maximum likelihood. Response variables represent the relative frequency of the number of transitions per session.

	Predictor Variable	Estimate	Standard Error	Z-value	Pr (> z)
Model 1 Comparing Periods	Intercept	2.10	6.55×10 ⁻²	32.12	<0.0001***
	Before	1.28×10 ⁻²	5.10×10 ⁻²	2.51	1.22×10⁻²*
	After	8.28×10 ⁻²	4.65×10 ⁻²	1.78	7.17×10 ⁻¹
	Adult Male	2.74×10 ⁻¹	1.08×10 ⁻¹	2.53	1.15×10 ⁻² *
	Infant	3.13×10 ⁻¹	1.08×10 ⁻²	2.90	3.78×10 ⁻³ **
	Before*Adult Male	-7.11×10 ⁻²	8.43×10 ⁻²	-0.84	3.99×10 ⁻¹
	After*Adult Male	-7.07×10 ⁻²	7.65×10 ⁻²	-0.92	3.55×10 ⁻¹
	Before* Infant	-6.27×10 ⁻²	8.27×10 ⁻²	-0.76	4.49×10 ⁻¹
	After* Infant	-2.10×10 ⁻²	7.57×10 ⁻²	-0.28	7.83×10 ⁻¹
Model 2 Comparing Distances to tourists during visits	Intercept	1.86	5.72×10 ⁻²	32.48	<0.0001***
	During >3m	-2.86 ×10 ⁻¹	5.46×10 ⁻²	-5.24	1.61×10 ⁻⁷ ***
	Adult Male	3.02 ×10 ⁻¹	9.14×10 ⁻²	3.31	9.34×10 ⁻⁴ ***
	Infant	3.88×10 ⁻¹	9.26×10 ⁻²	4.19	2.80×10 ⁻⁵ ***
	During >3m* Adult Male	-3.26×10 ⁻¹	8.74×10 ⁻²	-3.73	1.95×10 ⁻⁴ ***
	During >3m* Infant	-1.25×10 ⁻¹	8.76×10 ⁻²	-1.43	1.53×10 ⁻¹
Model 3 Comparing Higher Distances to tourists during visits	Intercept	1.70	7.18×10 ⁻²	23.64	<0.0001***
	During 3-7 m	-2.19×10 ⁻¹	7.99×10 ⁻²	-2.74	6.12×10 ⁻³ ***
	Adult Male	-8.23×10 ⁻²	1.24×10 ⁻¹	-0.66	5.08×10 ⁻¹
	Infant	5.40×10 ⁻²	1.21×10 ⁻¹	0.45	6.10 ⁻¹
	During 3-7m* Adult Male	1.09×10 ⁻¹	1.36×10 ⁻¹	0.80	4.21×10 ⁻¹
	During 3-7m* Infant	3.22×10 ⁻¹	1.32×10 ⁻¹	2.45	1.44×10 ⁻¹ *

*Predictor variables included Period (*Before*, *During*, and *After*) and Class (*Adult females*, *Adult males*, and *Infants*) for Model 1; Distance 1 (*During >3 m* and *During >3 m*) and Class (*Adult females*, *Adult males*, and *Infants*) for Model 2; Distance 2 (*During 3–7 m* and *During >7 m*) and Class (*Adult females*, *Adult males*, and *Infants*) for Model 3. Comparisons were made against the intercept of the first levels of each factor (Period = *During*, Age-sex class = *Adult female*, Distance = *During >3 m*, Distance 2 = *During >7 m*). Individual identity was entered as a random effect in both models. Data are based on 3661 observations of behavioral transitions in 15 individuals in Model 1; based on 1626 observations of 15 individuals in Model 2; based on 811 observations of 15 individuals in Model 3. Pr (>|z|) values denote the level of statistical significance, with * indicating p < 0.05, ** indicating p < 0.01, and *** indicating p < 0.001.

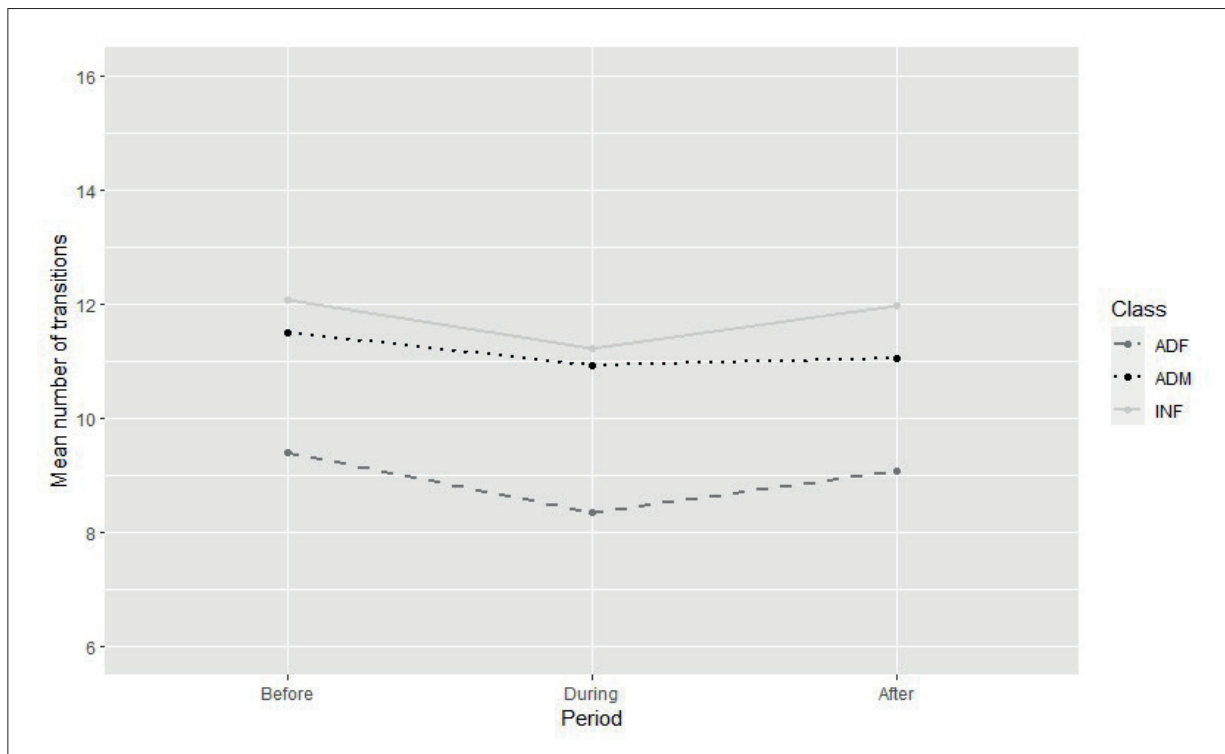


Figure 1. Mean number of behavioral transitions per age-sex class in each period of presence and proximity to tourists.

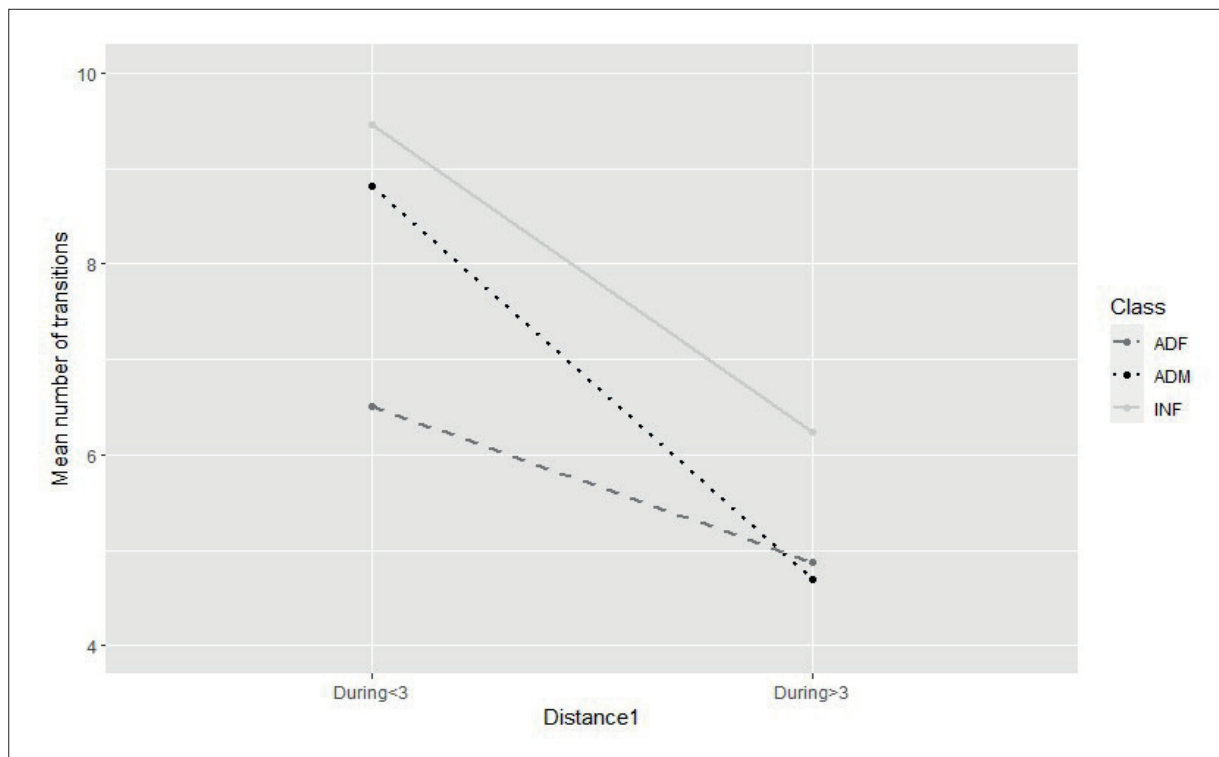


Figure 2. Mean number of behavioral transitions per age-sex class in close distances between tourists and gorillas (< 3m compared to > 3m).

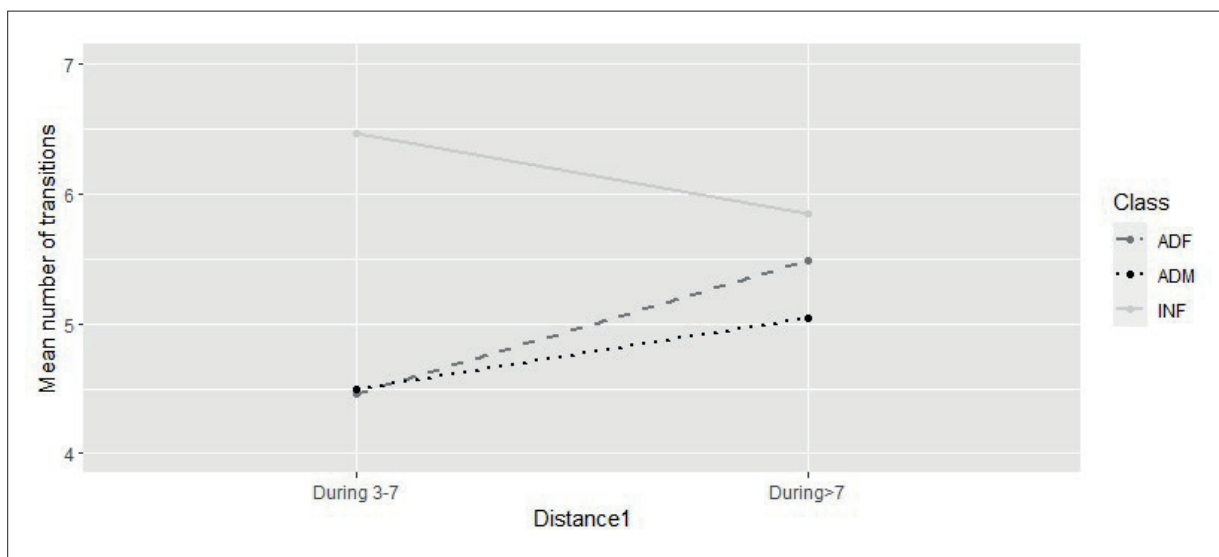


Figure 3. Mean number of behavioral transitions per age-sex class when comparing distances of 3–7 m and distances exceeding 7 m between tourists and gorillas.

such as scratching, affiliation, and human-directed behaviors are direct responses (i.e., transitions not occurring by chance) during tourist proximity, but the temporal organization of the behaviors depended on the age-sex class. The mean number of transitions decreased during the tourist visits (Fig. 1), but contrary to our expectations, gorillas showed higher than average transitions at shorter distances from tourists compared to the longer distances to tourists (Fig. 2). We anticipated that in close proximity to tourists (*during* < 3 m), gorillas would suppress transitions to

different behaviors, opting to spend more time employing coping strategies associated with close contact with humans (see Costa *et al.* 2023a, 2023b but see Kaburu *et al.* 2019; Marty *et al.* 2019 for similar use of coping mechanisms in rhesus and long-tailed macaques at short distances to tourists). In other words, we expected that spending more time performing coping strategies related to close contact with tourists could lead to a decline in the number of transitions when tourists are extremely close. Indeed, all age-class individuals showed significant transitions to human-directed,

agonistic, and fear-related behavior in the condition *during* <3 m (but not in the condition *during* >3 m, Table 2) consistent with previous results. However, the mean number of transitions overall (including all behaviors together) showed a peak *during* <3 m (Fig. 2). Increased levels of activity and motor restlessness have been demonstrated as behavioral indicators of anxiety in humans (World Health Organization 2023). This may also apply to gorillas. Moreover, gorillas shifted more often to interactions with humans at distances less than 3 m and they exhibited increased levels of activity (changing regularly from one behavior to another). Previous studies have also indicated that the rate of interactions with humans tends to occur predominantly within a distance of less than 3 m (Costa *et al.*, 2023b). In particular some of these interactions with humans to which gorillas transitioned (Table 2) were also associated with vigilance behavior (females) and other types of human-directed behavior (for example, direct interactions trigger human avoidance in infants, aggression to humans triggers directed interactions in males and females), which means that gorillas ceased spending time performing other typical behaviors to accommodate these interactions. Indeed, changes affecting specific behaviors that in turn affect other behavioral categories may limit the behavioral plasticity and entail conservation costs – to a point where the available responses may become maladaptive and potentially life-threatening (Mason *et al.* 2013; Sih 2014; Lopez-Sepulcre and Kokko 2012; Rubenstein 2016). Habituated mountain gorillas allow tourists to approach to within 7 m before moving away (Costa *et al.* 2023 but see Marechal *et al.* 2016 for similar results in Barbary macaques). Western lowland gorillas (Ando *et al.* 2008) under the process of habituation, allow researchers and trackers to approach no closer than 10 m from the group. With tourists spending most time of their viewing hours within 3 m (Costa *et al.* 2023a, 2023b) gorillas managed to switch to coping mechanisms that potentially attenuated the disturbance caused by the excessive proximity to humans but showed a less diverse repertoire of behavioral patterns.

The adult males showed a significant probability of transition to scratching during tourist visits when tourists were 3–7 m (*during* 3–7 m) away but this same trend for infants is true at shorter distances to tourists instead (*during* <3 m). This is surprising considering that looking at time spent scratching, adult males were the only significant age-sex class showing a significant peak in scratching behavior within 3 m of the tourists (although the entire group was found to scratch more in the presence of tourists) (Costa *et al.* 2023b). This means that infants may have shifted more often to this behavior at *during* <3 m but males spent more time performing the behavior or had to accommodate other behaviors (such as human interactions that occurred almost exclusively within 3 m of the tourists), which in turn diluted the frequency of transitioning to scratching. As such, the result of the transition patterns highlights the different attributes of how this stress indicator is present in adult males and infants. An alternative explanation is that scratching

behavior is also shown to reflect positive arousal (Neil and Caine 2016). Such arousal in the present context could be in the form of direct interactions with the tourists. This could be the case for infants, who have always replaced human-directed behavior with scratching during tourist visits when tourists were more than 3 m away and are, due to their immaturity, more naïve and curious towards different stimuli. However, tourists within <3 m of infants prompted avoidance, which seems to support the theory that such close interactions produce more fear/stress than positive arousal. Adult males and females, on the other hand, transitioned more often to inactivity *during* <3 m, which might reveal an increased need to be attentive to the surroundings; or may be due to the gorillas' natural cycle between feeding (in early hours) and resting (afterward).

Infants and adult males were also similar in the way they transitioned to affiliation during tourist visits more often than females. This does not mean that they used this coping mechanism more than females since there was no significant difference between age-sex classes in social behavior during tourist visits (Costa *et al.* 2023b) but rather that females may have spent potentially longer uninterrupted time performing affiliation during the tourists' visits. An alternative explanation is that males may seek the reinforcement of social connections during these moments to enhance group cohesion (Costa *et al.* 2023a) and infants may seek protection from the group when tourists are nearby. Across conditions, females showed greater flexibility of transitions (ranging from 18 to 27 significant transitions, Table 2), but lower diversity of transitions per session (Fig. 1). This means that despite showing flexibility to transition from one behavior to another, females take longer to move from one behavior to the other, which may be the reason of their low diversity for the 10-min focal observation sessions. For them, inactivity and feeding were the most common transitions. Because four of the six females in the group were breastfeeding during the data collection period, it is possible that the need for extra nutrition exceeded the need for stress relief. Mountain gorillas have abundant resources available and spend most of their time feeding (Rothman *et al.* 2007), which is the reason why the anthropogenic impact is potentially less severe on their feeding time compared to other species with more limited resources.

In sum, our results revealed that gorillas cope with the presence of tourists by switching to behaviors that may offer them some stress relief and social support during the perceived risk, in addition to previous evidence that has shown an increase in the percentage of time spent in such behaviors (Steklis *et al.* 2004; Muyambi 2005; Mabano *et al.* 2014; Costa *et al.* 2023a, 2023b). External factors may have confounded our results (the tourists' behavior or environmental factors such as different vegetation types or weather conditions) so we strongly recommend that future studies should include such parameters in their design as well as extend our research to other gorilla groups with different levels of habituation. Since the probabilities of behavioral transition

are independent of the time scale used, this tool adds a further advantage to the comparison of studies of different lengths. Together with previous findings, we show clear evidence of a change in the temporal pattern of behavior of mountain gorillas when in close proximity to tourists. In this case, the study of the behavioral sequences has provided us with more details on how gorillas may organize their activities during close encounters with tourists, compared to their absence and in relation to distance.

Mountain gorillas act as flagship and umbrella species in the region (Tumusiime and Vedeld 2012). Gorilla tourism would benefit from more restrained activity to reduce the negative consequences for gorilla welfare (for example, the enforcement of the safety distance rule of 7 m, by the use of more assertive messages (Gessa and Rothman 2021) and restrictive management of tourists during their viewing time. A recent examination of social media posts from gorilla tourists reveals a rise in images depicting physical contact between tourists and gorillas (van Hamme *et al.*, 2021). This suggests that tourists perceive such close interactions as acceptable, potentially influenced by the prevalence of these online images. To address this, we recommend incorporating a preventive measure during the permit acquisition process. Specifically, at the point of solicitation and payment for the tracking permit, tourists should be requested to sign the Gorilla Friendly™ Pledge. Additionally, they should be provided with a concise but firm list detailing potential diseases transmitted by humans, accompanied by actual photographs of sick animals. Furthermore, graphical representations of stress indicators (e.g., Costa *et al.*, 2023b), illustrating the increased stress animals experience in close proximity to tourists, should be included to persuade tourists who do not feel they may transmit diseases to the animals. Conversely, the evaluation of the performance of guides and trackers during visits should not solely rely entirely on the satisfaction of the tourists. It should also consider their adherence to recommended guidelines. Guides and trackers who demonstrate high levels of compliance with these recommendations should be rewarded.

The implementation of the rules of Ecotourism designed to prevent animals from getting too accustomed to being in close proximity to humans is also vital to promote economic sustainability. In Bwindi, gorillas only rarely ranged outside the forest to raid farmers' crops before the forest was gazetted a national park (Madden 2006). Ever since the initiation of ecotourism, habituated gorillas have increased their visits to local farmers' agricultural fields on the border with the national park (pers observ.; Madden 2006; Seiler and Robbins 2016). This habituation to humans increases the pathogen-transmission risk exponentially besides aggravating conflict with local populations. Indeed, the people's tolerance for certain species may change quickly following economic change (Hockings and McLennan 2014). Farmers affected by crop raiding, for instance, may respond negatively (or even aggressively) to Bwindi gorillas invading their crops (Madden 2006). On the other hand, the

economic benefits of tourism may become inconsistent. With the severe reduction of tourism and decline in income due to the COVID-19 pandemic, the local population turned again to illegal hunting inside the park borders. In the first months of the pandemic in 2020, the Uganda Wildlife Authority reported a doubling of the number of recovered snares and cases of poaching, even though the patrol effort in protected areas in Uganda remained unchanged, including in Bwindi Impenetrable National Park (John 2021). To address this concern, and considering the increased number of new habituated groups in the last decade, we recommend discontinuing the habituation of new gorilla groups to safeguard an unhabituated wild population. We also recommend increasing the diversity of tourist activities towards other species and the natural resources in the region, in addition to investment in farming in the agriculture sector. Making equity investments in local crop producers, may also benefit the local community by decreasing its dependency on Mountain gorilla tourism. Direct engagement of the local community with conservation and research projects outside the Tourism sector, such as mapping forest densities, measuring canopy disturbances, continued use of transects to monitor species abundance and distribution, may also provide stable employment and chances for education to local communities.

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Author Contributions

All authors conceived the research; R. C. collected data; R. C. and A. B. ran the analysis; R. C. led the manuscript writing process; R. C. prepared figures; and all authors contributed to the manuscript with edits, comments, and interpretation of results.

Data Availability

The data sets analyzed in the current study are available from the corresponding author on reasonable request.

Supplementary Material

Available at:

<http://www.imate-sg.org/storage/pdf/PC37_Costa_et_al_gorilla_tourism_Suppl_Mat.pdf>

Table S1. Distribution of observation sessions (10 minutes focal) per individual: before, during and after the tourist hour.

Table S2. (a). Summary of the relative probabilities of occurrence of first above-chance transitions in adult females.

Table S2 (b). Summary of the relative probabilities of occurrence of first above-chance transitions in adult males.

Table S2 (c). Summary of the relative probabilities of occurrence of first above-chance transitions in infants.

Literature Cited

Alados, C. L., J. M. Escos and J. M. Emlen. 1996. Fractal structure of sequential behaviour patterns: an indicator of stress. *Anim. Behav.* 51(2): 437–443.

Ando, C., Y. Iwata and J. Yamagiwa. 2008. Progress of habituation of western lowland gorillas and their reaction to observers in Moukalaba-Doudou National Park, Gabon. *Afr. Study Monogr. Supplementary Issue* 39: 55–69.

Asher, L., L. M. Collins, A. Ortiz-Pelaez, J. A. Drewe, C. J. Nicol and D. U. Pfeiffer. 2009. Recent advances in the analysis of behavioural organization and interpretation as indicators of animal welfare. *J. Roy. Soc. Interface* 6(41): 1103–1119.

Brandão, A., R. Costa, E. Rodrigues and L. Vicente. 2019. Using behaviour observations to study personality in a group of capuchin monkeys (*Cebus apella*) in captivity. *Behaviour* 156(3–4): 203–243.

Banerjee, A., N. Ghosh and A. Bhadra. 2021. Power-laws in dog behavior may pave the way to predictive models: a pattern analysis study. *Heliyon* 7: 1–6.

Bateman, P. W. and P. A. Fleming. 2017. Are negative effects of tourist activities on wildlife over-reported? A review of assessment methods and empirical results. *Biol. Conserv.* 211: 10–19.

Berman, C. M., M. D. Matheson, J. H. Li, H. Ogawa and C. S. Ionica. 2014. Tourism, infant mortality and stress indicators among Tibetan macaques at Huangshan, China. In: *Primate Tourism: A Tool for Conservation?* A. E. Russon and J. Wallis (eds.), pp.21–43. Cambridge University Press, Cambridge, UK.

Boonstra, R. 2013. Reality as the leading cause of stress: rethinking the impact of chronic stress in nature. *Funct. Ecol.* 27(1): 11–23.

Brooks, M. E., K. Kristensen, K. J. van Benthem, A. Magnusson, C. W. Berg, A. Nielsen, H. J. Skaug, M. Maechler and B. M. Bolker. 2017. glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *R J.* 9(2): 378–400.

Brown, M. B. 1974. The identification of sources of significance in two-way contingency tables. *Appl. Stat.* 23: 405–413.

Caspi, T., J. R. Johnson, M. R. Lambert, C. J. Schell and A. Sih. 2022. Behavioral plasticity can facilitate evolution in urban environments. *Trends Ecol. Evol.* 37: 1092–1103.

Chapman, C. A., D. Twinomugisha, J. A. Teichroeb, K. Valenta, R. Sengupta, D. Sarkar and J. M. Rothman. 2016. How do primates survive among humans? Mechanisms employed by vervet monkeys at Lake Nabugabo, Uganda. In: *Ethnoprimatology: Primate Conservation in the 21st Century*, M. T. Waller (eds.), pp. 77–94. Springer, Cham.

Cordero-Rivera, A. 2017. Behavioral diversity (ethodiversity): a neglected level in the study of biodiversity. *Front. Ecol. Evol.* 5: 1–7. doi.org/10.3389/fevo.2017.00007

Costa, R. F., V. Romano, A. S. Pereira, J. D. Hart, A. MacIntosh and M. Hayashi. 2023a. Mountain gorillas benefit from social distancing too: close proximity from tourists affects gorillas' sociality. *Conserv. Sci. Pract.* 5: e12859

Costa, R., R. S. Takeshita, M. Tomonaga, M. A. Huffman, G. Kalema-Zikusoka, F. Bercovitch and M. Hayashi. 2023b. The impact of tourist visits on mountain gorilla behavior in Uganda. *J. Ecotourism*, 1–19. doi.org/10.1080/14724049.2023.2176507

de la Torre, S. 2014. Effects of tourism on Ecuadorian primates: is there a need for responsible primate tourism? In: *Primate Tourism: A Tool for Conservation?* A. E. Russon and J. Wallis (eds.), pp. 245–255. Cambridge University Press, Cambridge, UK.

- Deakin, A. G., J. W. Spencer, A. R. Cossins, I. S. Young and L. U. Sneddon. 2019. Welfare challenges influence the complexity of movement: fractal analysis of behaviour in zebrafish. *Fishes* 4(1): 8.
- Fresneau, N. and W. Müller. 2019. Flexible communication within bird families—The consequences of behavioural plasticity for parent–offspring coadaptation. *Ecol. Evol.* 9(1): 693–702.
- Gessa, S. J. and J. M. Rothman. 2021. The importance of message framing in rule compliance by visitors during wildlife tourism. *Conserv. Sci. Pract.* 3(10): 1–8.
- Geffroy, B., D. S. Samia, E. Bessa and D. T. Blumstein. 2015. How nature-based tourism might increase prey vulnerability to predators. *Trends Ecol. Evol.* 30(12): 755–765.
- George, S. A., M. Rodriguez-Santiago, J. Riley, J. L. Abelson, S. B. Floresco and I. Liberzon. 2015. Alterations in cognitive flexibility in a rat model of post-traumatic stress disorder. *Behav. Brain Res.* 286: 256–264.
- Grossberg, R., A. Treves and L. Naughton-Treves. 2003. The incidental ecotourist: measuring visitor impacts on endangered howler monkeys at a Belizean archaeological site. *Environ. Conserv.* 30(1): 40–51.
- Hockings, K. J., M. R. McLennan and C. Hill. 2014. Fear beyond predators. *Science* 344: 981–981.
- Japayassú, H. F., C. C. Alberts, P. Izar and T. Sato. 2006. EthoSeq: a tool for phylogenetic analysis and data mining in behavioral sequences. *Behav. Res. Methods* 38(4): 549–556.
- John, W. F. 2021. Coronavirus pandemic threat to the conservation of protected areas and local community well-being: a case of Bwindi Impenetrable National Park. *J. Hosp. Tour.* 19(1): 78–90.
- Kabano, P., J. Arinaitwe and M. M. Robbins. 2014. History of Habituated Gorillas in Bwindi. *Gorilla J.* 30: 14–15.
- Kaburu, S. S. *et al.* 2019. Interactions with humans impose time constraints on urban-dwelling rhesus macaques (*Macaca mulatta*). *Behavior* 156(12): 1255–1282.
- Klailova, M., C. Hodgkinson and P. Lee. 2010. Behavioral responses of one western lowland gorilla (*Gorilla gorilla gorilla*) group at Bai Hokou, Central African Republic, to tourists, researchers and trackers. *Am. J. Primatol.* 72: 897–906.
- Kembro, J. M., M. A. Perillo, P. A. Pury, D. G. Satterlee and R. H. Marin. 2009. Fractal analysis of the ambulation pattern of Japanese quail. *Br. Poult. Sci.* 50(2): 161–170.
- Lopez-Sepulcre, A. and H. Kokko. 2012. Understanding behavioural responses and their consequences. In: *Behavioural Responses to a Changing World: Mechanisms and Consequences*, U. Candolin and B. B. Wong (eds.), pp. 3–15. Oxford University Press, Oxford.
- Lucass, C., P. Korsten, M. Eens and W. Müller. 2016. Within-family parent–offspring co-adaptation in a wild bird: on static traits, behavioural reaction norms, and sex differences. *Funct. Ecol.* 30(2): 274–282.
- Lunardi, D. G. and R. G. Ferreira. 2013. Group composition influences on behavioral sequence patterns of the Guiana dolphin *Sotalia guianensis*. *J. Ethol.* 31: 49–53.
- Mabano, A. 2013. Impact of Tourists on Mountain Gorilla Behavior. Bachelor dissertation, National University of Rwanda, Rwanda.
- Macfie, E. J. and E. A. Williamson. 2010. *Best Practice Guidelines for Great Ape Tourism*. IUCN/SSC Primate Specialist Group, Gland, Switzerland.
- MacIntosh, A. J., C. L. Alados and M. A. Huffman. 2011. Fractal analysis of behaviour in a wild primate: behavioural complexity in health and disease. *J. Roy. Soc. Interface* 8(63): 1497–1509.
- MacIntosh, A. J. 2014. The fractal primate: interdisciplinary science and the math behind the monkey. *Prim. Res.* 30(1): 95–119.
- Madden, F. 2006. Gorillas in the garden: human–wildlife conflict at Bwindi Impenetrable National Park. *Policy Matters* 14: 180–190.
- Majolo, B., E. van Lavieren, L. Maréchal, A. MacLarnon, G. Marvin, M. Qarro, and S. Semple. 2013. Out of Asia: The singular case of the Barbary macaque. In: *The Macaque Connection*, A. Sinha, M. A. Huffman and S. Radhakrishna (eds.), pp.167–183. Springer, New York.
- Maréchal, L., A. MacLarnon, B. Majolo and S. Semple. 2016. Primates’ behavioral responses to tourists: evidence for a trade-off between potential risks and benefits. *Sci. Rep.* 6: 32465.
- Martin, P. and P. Bateson. 2007. Recording methods. In: *Measuring Behavior: An Introductory Guide*. Cambridge University Press, Cambridge, UK.
- Marty, P. R. *et al.* 2019. Time constraints imposed by anthropogenic environments alter social behavior in longtailed macaques. *Anim. Behav.* 150: 157–165.
- Mason, G., C. C. Burn, J. A. Dallaire, J. Kroshko, H. M. Kinkaid, H. M., and J. M. Jeschke. 2013. Plastic animals in cages: behavioural flexibility and responses to captivity. *Anim. Behav.* 85(5): 1113–1126.
- Miller, L. J., L. K. Lauderdale, J. L. Bryant, J. D. Mellen, M. T. Walsh and D. A. Granger. 2021. Behavioral diversity as a potential positive indicator of animal welfare in bottlenose dolphins. *PLoS One* 16(8): e0253113.
- Monaghan, P. and M. F. Haussmann. 2015. The positive and negative consequences of stressors during early life. *Early Hum. Develop.* 91(11): 643–647.
- Neal, S. J. and N. G. Caine. 2016. Scratching under positive and negative arousal in common marmosets (*Callithrix jacchus*). *Am. J. Primatol.* 78(2): 216–226.
- Nowak, K. and P. C. Lee. 2013. “Specialist” primates can be flexible in response to habitat alteration. In: *Primates in Fragments: Complexity and Resilience*, L. K. Marsh and C. A. Chapman (eds.), pp. 199–211. Springer, New York.
- Ogden, J. *et al.* 1991. Compilation of gorilla ethograms. Atlanta, Georgia: Gorilla Species Survival Plan, Gorilla Behavior Advisory Group.

- Reser, J. E. 2016. Chronic stress, cortical plasticity and neuroecology. *Behav. Process.* 129: 105–115.
- Rothman, J. M., E. S. Dierenfeld, H. F. Hintz and A. N. Pell. 2008. Nutritional quality of gorilla diets: consequences of age, sex, and season. *Oecologia* 155(1): 111–122.
- Rubenstein, D. 2016. Anthropogenic impacts on behaviour: the pros and cons of plasticity. In: *Conservation Behaviour*, O. Berger-Tal and D. Saltz (eds), pp. 121–146. Cambridge University Press, Cambridge, UK.
- R Core Team 2023. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL <https://www.R-project.org/>.
- Seiler, N. and M. M. Robbins. 2016. Factors influencing ranging on community land and crop raiding by mountain gorillas. *Anim. Conserv.* 19(2): 176–188.
- Sih, A. 2013. Understanding variation in behavioural responses to human-induced rapid environmental change: a conceptual overview. *Anim. Behav.* 85(5): 1077–1088.
- Steiner, U. K. and J. Van Buskirk. 2008. Environmental stress and the costs of whole-organism phenotypic plasticity in tadpoles. *J. Evol. Biol.* 21(1): 97–103.
- Steklis H. D., C. Hodgkinson, K. Fawcett, N. Gerald Steklis, N. Czekala, A. Lilly and P. T. Mehlman. 2004. The impact of tourism on mountain gorillas. *Folia Primatol.* 75: 40–41.
- Thatcher, H. R., C. T. Downs and N. F. Koyama. 2019. Positive and negative interactions with humans concurrently affect vervet monkey (*Chlorocebus pygerythrus*) ranging behaviour. *Int. J. Primatol.* 40(4–5): 496–510.
- Thatcher, A. and N. Insel. 2021. Variability of social interactions in new and established relationships in female degus. *bioRxiv*, 2021-08.
- Thompson, N. A. and M. Cords. 2018. Stronger social bonds do not always predict greater longevity in a gregarious primate. *Ecol. Evol.* 8(3): 1604–1614.
- Tumusiime, D. M. and P. Vedeld. 2012. False promise or false premise? Using tourism revenue sharing to promote conservation and poverty reduction in Uganda. *Conserv. Soc.* 10(1): 15–28.
- van Baaren, J. and U. Candolin. 2018. Plasticity in a changing world: behavioural responses to human perturbations. *Curr. Opin. Insect Sci.* 27: 21–25.
- Van Buskirk, J. 2012. Behavioural plasticity and environmental change. In: *Behavioural Responses to a Changing World: Mechanisms and Consequences*, U. Candolin and B. B. Wong (eds.), pp. 145–158. Oxford University Press, Oxford.
- Van Hamme, G., M. Svensson, T. Q. Morcatty, K. A. I. Nekaris and V. Nijman. 2021. Keep your distance: using Instagram posts to evaluate the risk of anthroponotic disease transmission in gorilla ecotourism. *People and Nature* 3(2): 325–334.
- Wright, P. C., B. Andriamihaja, S. J. King, J. Guerriero and J. Hubbard. 2014. Lemurs and tourism in Ranomafana National Park, Madagascar: economic boom and other consequences. In: *Primate Tourism: A Tool for Conservation?* A. E. Russon and J. Wallis (eds.), pp.123–146. Cambridge University Press, Cambridge, UK.
- Weber, A., G. Kalema-Zikusoka and N. J. Stevens. 2020. Lack of rule-adherence during mountain gorilla tourism encounters in Bwindi Impenetrable National Park, Uganda, places gorillas at risk from human disease. *Public Health Front.* 8(1). doi: 10.3389/fpubh.2020.00001
- Wickham, H. 2016. *ggplot2: Elegant Graphics for Data Analysis*. Springer, New York. <https://ggplot2.tidyverse.org>.
- Williamson, E. A. and N. Gerald-Steklis. 2001. Composition of *Gorilla gorilla beringei* groups monitored by Kari-soke Research Center. *Afr. Primates* 5: 48–51.
- Whitehead, H. 2010. Conserving and managing animals that learn socially and share cultures. *Learn. Behav.* 38(3): 329–336.
- World Health Organization. 2023. International Classification of Diseases (ICD): [ICD-11 for Mortality and Morbidity Statistics: 6B00 Generalised anxiety disorder]. Website: <<http://id.who.int/icd/entity/1712535455>>. Accessed 13 October 2023.
- Wright, E. and M. M. Robbins. 2014. Proximate mechanisms of contest competition among female Bwindi mountain gorillas (*Gorilla beringei beringei*). *Behav. Ecol. Sociobiol.* 68(11): 1785–1797.

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