7. PORTFOLIO IPE

Notre équipe présente la particularité de mener des recherches à la fois *ex situ* et *in situ* et appuie une grande partie de ses travaux sur des données longitudinales collectées sur les primates dans leurs habitats naturels, en Afrique (Madagascar, RDC, RCA, Cameroun, Ouganda) et en Asie (Indonésie, Japon). À ce titre, les stations de terrain jouent un rôle-clé et sont des outils indispensables et précieux permettant de conduire des recherches originales et de long-terme sur plus d'une dizaine d'espèces de primates.

Les publications choisies pour ce portfolio illustrent la diversité des travaux réalisés au sein de l'équipe, ainsi que l'approche interdisciplinaire de nos travaux et notamment notre double approche à la fois théorique et expérimentale. Ces publications ont permis de réunir plusieurs membres statutaires de l'équipe et de l'UMR (**en gras**), voire du MNHN, que ce soit des chercheur.e.s, des post-doctorant.e.s, des doctorant.e.s et étudiant.e.s, mais également des ingénieur.e.s.

<u>7.1</u>



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<u>7.2</u>



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Primate–Predator Interactions: Is There a Mismatch Between Laboratory and Ecological Evidence?

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Abstract

Abundant empirical and theoretical studies indicate that predation is a key driver of primate evolution. The Snake Detection Theory (SDT) posits that snakes have been the main predators of primates since the late Cretaceous and that they influenced the diversification and evolution of primates. Laboratory research focusing on the innate ability of primates to detect snakes amid complex visual stimuli has provided strong support for key tenets of the SDT. While this theory has greatly contributed to our knowledge of primate evolution, supporting experimental studies may have overly focused on snakes and disregarded other important predators. This potential sampling bias weakens the conclusion that primates respond with a specific (high) intensity to snakes compared to other predators. We reviewed the literature about primate-predator interactions under natural and experimental conditions. We listed the primate and predator species involved in natural versus experimental studies. Predation events on primates recorded in the field mainly involved other primates, then raptors and carnivorans. SDT-related experimental studies heavily focused on snakes as predator stimuli and did not include raptors. Other experimental studies largely used snakes and primates and to a lesser extent carnivorans. Apes were the most often tested primates in experimental studies, whereas other primate taxa were neglected. Moreover, predators used as stimuli in experimental studies were inaccurately identified, notably snakes. Altogether, our results show that SDT-related studies neglected most of the major natural predators of primates. SDT studies also focused on a handful of primate species, whereas the theory relies on comparisons among taxa. Finally, poor taxonomic information on snakes used as stimuli blurs the interpretation of their relationship with primates. We suggest that future studies test the SDT by presenting a wide range of predators to different primate species to improve our understanding of the complexity of predator-prey interactions.

Keywords Snake detection theory · Predation · Primate evolution · Visual cues

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Introduction

The selective pressures exerted by predators rank amongst the most powerful evolutionary forces and are capable of rapidly transforming phenotypes (Darimont et al., 2009). There is a broad consensus that predators are one of the most important drivers of primate evolution (Cartmill, 1992; Gursky-Doyen & Nekaris, 2007; Mcgraw & Berger, 2013). Using extensive ecological, genetic, physiological, neuroanatomical, behavioural, and paleontological information, Isbell (2006) developed a comprehensive theory focused on predator-prey interaction. The Snake Detection Theory (SDT) posits that for the past 100 million years (My), snakes were the principal predators of mammals, including early primates, and exerted strong selective pressures on primates. The SDT proposes that besides high predation rates exerted by constrictor snakes, venomous snakes introduced an additional major risk in a broad Afro-Eurasian context. This risk is thought to have promoted an arm race between snakes and primates and was "ultimately responsible for the emergence of anthropoids" (Isbell, 2006: p.12). More precisely, the SDT proposes that primates evolved an outstanding ability to detect concealed, motionless snakes before their fatal strike, and that primates acquired specific traits, such as stereoscopic trichromatic colour vision and an enlarged brain, to quickly process the massive amount of information generated (Isbell, 2006). Formalized in 2006, the SDT was extended to other human traits in 2009, including social and cultural traits (Isbell, 2009). A central tenet of the SDT, the capacity to detect snake stimuli more rapidly than other stimuli, has been validated experimentally in human and nonhuman primates (Le et al., 2014; Soares et al., 2014; Van Strien & Isbell, 2017; Weiss *et al.*, 2015). Further research suggested that the remarkable capacity of primates and most notably humans to detect snakes, along with the sophisticated dedicated underlying neuronal structures, is innate and results from strong selection (Kawai, 2019).

Recently, however, the SDT has been challenged (Silcox & López-Torres, 2017; Wheeler, 2010). For example, a study using pupil dilation (mydriasis) in infants, which suggested an innate fear of snakes (Hoehl *et al.*, 2017), was questioned, because this physiological response does not necessarily correlate with fear or negative stimuli (Denzer, 2018). Studies suggesting that the strong reactions elicited by snakes stimuli are specific and hard-wired (Gomes *et al.*, 2017) were also challenged when similar strong reactions were obtained using bicycles and cars instead of snakes (Gayet *et al.*, 2019). Moreover, a lack of relationship between the degree of orbital convergence in primates and the duration of shared history with venomous snakes favoured different visual ability among primate taxa (Wheeler *et al.*, 2011). Other authors have argued that the human visual detection and withdrawal reflex following snake detection are too slow to prevent bites in natural settings (Coelho *et al.*, 2019).

A central assumption of the SDT is that snakes were the first predators of early primates and that other classes of predators did not affect the evolution of early primates due to their late emergence (Isbell, 2006, 2009; Kawai, 2019). This

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assumption is not supported by any paleontologically established facts and is thus debatable. It is likely that various groups of carnivorous mammals and birds were major predators of primates from their emergence (Brusatte et al., 2015; Choiniere et al., 2021; Wilson et al., 2016) until recent times (Berger & Mcgraw, 2007; Camarós et al., 2015; McGraw et al., 2006; Zuberbühler & Jenny, 2002). Moreover, if primates emerged in the late Cretaceous, as genetic data suggest, then it seems likely that they would have been preyed on by various theropods that ruled terrestrial ecosystems. Carnivorans and raptors, therefore, may have deeply influenced primate evolution, as hypothesized by a study that found better detection of carnivores in trichromatic human subjects than in dichromatic ones (de Moraes et al., 2021). Therefore, besides snakes, it is important to include other major predators of primates, such as carnivorans, raptors, and crocodilians (which evolved long before early primates: Grigg & Kirshner, 2015), in experimental studies. Moreover, encompassing the diversity of primate predators is essential to assess the extent to which snakes elicit specific antipredator responses, ranging from detection to behaviours; otherwise we cannot distinguish the SDT from a more general predator detection theory.

It is equally critical to test a phylogenetic and taxonomic diversity of primates in experimental studies. There are 79 genera and approximately 500 species of extant primates (Estrada *et al.*, 2017; Mittermeier *et al.*, 2013). Strepsirrhines comprise 27% of primate species; Pan-American monkeys 35%, Afro-Eurasian monkeys (excluding great apes) 37%, and great apes just 1%. The distinction and characterization of these groups is central to the SDT, because it holds that the divergent evolutionary routes among these primate species were caused by different assemblages of snakes (especially venomous snakes) across biogeographical areas (Isbell, 2006).

Finally, it is important to consider the taxonomic accuracy used by experimenters within and among studies and to use the most precise taxonomic level to describe the predatory stimuli presented to the primates tested. Most primate predators can be easily identified. Few carnivores are large enough to regularly feed on primates. Few raptors specialize on primates. Most dangerous snakes are recognizable, and the low diversity of crocodiles greatly simplifies identification. In experimental studies, each species therefore should be named to the species or subspecies level without technical difficulty. For a large primate, the risk and threat of encountering a small cat *versus* a leopard are quite different, rendering accurate identification of predators during experimental tests an important parameter. Taxonomic inaccuracy makes it impossible to account for the differential reactions of primates facing different types of predators.

To address these issues, we scrutinized the scientific literature on primate-predator interactions. For each study, we recorded which stimulus and subjects (primates) were observed in natural conditions (observational studies) or used in experimental settings (experimental studies). For experimental studies, we considered whether the authors aimed to test the SDT (SDT studies) or had other objectives (Non-SDT studies). First, we assessed whether the stimuli presented in SDT and Non-SDT experimental studies differed and whether they matched the types of predators encountered by primates in natural conditions (Q1). Second, we compared the range of primates tested in SDT and Non-SDT experimental studies (Q2). Third, we assessed the taxonomic accuracy used to describe the predators observed in the wild or used as stimuli and presented to primates during experiments in SDT and Non-SDT studies (Q3). Observations of predation recorded in the wild are essential to evaluate the ecological relevance of the stimuli used and of the primate species tested in experimental studies (Non-SDT and SDT). Moreover, comparing Non-SDT studies and studies based on primate–predator interactions recorded in the wild provides an opportunity to examine the methodological choices that characterize SDT publications.

Methods

Selection of Publications

We used the PRISMA method to perform a systematic and reproducible literature survey (Page et al., 2021a, b). We used different combinations of keywords and adopted automatic procedures to extract scientific articles from JSTOR, ScienceDirect, Springer, Web of Science Core Collection, Wiley Online Library and Google Scholar databases (Table I). From the total number of articles extracted (N=18,153,145), automatic and manual procedures enabled us to discard out-offocus publications and to retain 201 studies that we could allocate to experimental versus observational categories. We examined the selected articles and retained those that evaluated the ability of primates to detect a specific stimulus (e.g., predator, dangerous/harmless animal or neutral), measured the fear level elicited by a stimulus, examined antipredator behaviour(s) in laboratory, captivity or the wild, or that reported clear predation cases. We only included original experimental or observational studies and discarded reviews except one (see below). For experimental studies, we narrowed our focus to visual stimuli, because vision is central to SDT, and more generally to hypotheses for primate evolution (Cartmill, 1992; Pessoa et al., 2014; Sussman, 2017). We excluded studies that considered the response of primates to auditory or chemical stimuli. Although these stimuli play important roles in primates to inform congeners about predatory threats for example (Fichtel & Kappeler, 2002), and their exclusion may influence the prevalence of specific stimulus types, they were out of the scope of the current investigation. We also used a comprehensive list of references from a book chapter that provided a review of predation events in primates, including reports that were not detected with our automated procedures (Miller & Treves, 2011). Further details of the search procedure are provided in the supplementary material (Online Resource 1, Figs. 5 and 6).

For observational studies, we searched for publications reporting direct observations of attempted predation events (successful or not) on primates in natural settings and indirect events with sufficient evidence to disregard scavenging. After screening, we retained 76 publications. We categorized these publications into the Predation group.

For experimental studies, we retained 125 articles that we subsequently allocated into two groups. SDT studies included publications explicitly framed around the SDT, or where the results were interpreted in this context (Isbell, 2006 or Isbell, 2009 had to be referenced in the bibliography). Non-SDT studies included

Table I Search words e. lications selected for ea bibliographic database. analysed $(N = 201)$, beca	mployed for the selection of experimen- ch bibliographic database and a book. Note that the total number of selected use several publications appeared repeared repeared repeared repea	ntal studies chapter (Mi publications atedly throu	and publications iller & Treves, 20 s displayed in this gh different combi	reporting pre 11). We limi table $(N=36$ nations	dation attempts up ted searching to the 57) does not corresp	on prima e first 100 pond to th	es in the wild and articles per searc e final total numb	l number of pub- h words for each er of publications
Search session	Search words	JSTOR	Science Direct	Springer	Web of Science	Wiley	Google Scholar	Miller & Treves
Experimental studies	Primates Fear Predators	5	14	14	18	7	12	I
	Primates Detection Predators	7	13	8	14	8	13	I
	Primates Antipredator Behaviors OR Behaviours	٢	4	L	6	S	8	I
	Snake Detection Theory	5	19	6	20	7	32	I
Predation studies	Predation on Primates	5	2	13	10	9	10	47
	Animals Attack Humans	1	0	0	6	1	1	ı

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publications that did not make explicit reference to the SDT. To precisely compare Non-SDT and SDT studies, we limited our search to the time period 2006–2022, after the first SDT publication (Isbell, 2006). Overall, we selected 201 articles (Predation, N=76; SDT, N=59; Non-SDT, N=66).

Data Extraction and Categorization of Variables

In all groups, we considered each encounter between a primate or a group of primates and a stimulus as an interaction (I). We retained only unambiguous interactions where both the stimulus and the subject(s) were described. Because SDT is strictly based on visual signals and taxidermized animals also may carry strong odors triggering antipredator response and acting as confounding factors, we decided to exclude this type of stimulus, as well as auditory stimulus. This choice resulted in the exclusion of only 12 interactions and four "Non-SDT" studies, which is unlikely to change the results. The number of "Non-SDT" studies considered was 62, and the total number of publications analysed was 197. The mean number of interaction(s) per article was 50 (standard deviation [SD] = 122.31; standard error of the mean [SEM] = 8.71; range: 1–1,254). The total number of interactions recorded was higher than the total number of articles scrutinized (N=9.816 interactions in 197 articles). For brevity, we pooled non-animal stimuli, such as plants, fungi, and objects, into a single category named "items." Items were generally used as controls. The accuracy in describing animal stimuli provided in the methods section of the articles varied greatly: for example, some studies gave scientific names, whereas others gave only very crude information. We assigned each animal stimulus to the most precise possible taxonomic level, typically ranging from species to order. We considered the ecological prey-predator context rather than phylogenetic relationships to pool stimuli into categories. For example, we treated crocodiles, which are more closely related to birds than to squamates, as a distinct group, because they represent a unique threat to primates. We summarized the resulting categorization in Online Resources 1 (Table S1) and 2. Depending on the question examined, we used ecological groups, taxonomic groups, or the most precise taxonomic information available. The distinction between strepsirrhines, Pan-American monkeys (platyrrhines), Afro-Eurasian monkeys, and apes (catarrhines) is central to the SDT; we therefore categorized primate species accordingly.

Study Questions

Q1: Do Stimuli Used in Experimental Studies Include the Main Predators Encountered by Primates in the Wild?

Some interactions (notably predation events) might be difficult to observe (Isbell, 1994), and observational biases affect which predation events can be witnessed. In addition, it is not always easy to combine scientific, anecdotal, and nonscientific predation reports. Nonetheless, the choice of predator stimuli used in experimental studies should be based on prey-predator interactions documented in the field

or inferred from indirect evidence of predation (discarding scavenging). Therefore, we used predation events in the wild (Predation studies) as a crude ecological baseline. Although such reports do not provide accurate predation rates because observation biases cannot be controlled for, they provide direct and reliable information that can be easily quantified. For example, abundant reports of leopards hunting monkeys show that this large felid represents a strong predatory threat to primates; such reports can be counted. We conducted two complementary analyses: a) we compared the main types of predators reported in Predation studies versus those used in Non-SDT and SDT studies; b) we assessed and compared the diversity of visual stimuli used in Non-SDT and SDT studies, notably the variety of predators, nonpredator animals, and various items (e.g., objects, plants). Because experimental studies evaluating the SDT are likely to compare primate responses to snakes, it is likely that snakes will be the most commonly used predators in SDT studies compared with Non-SDT studies. However, other animals, especially predators (e.g., carnivorans, raptors), should be used to evaluate the extent to which reactions are snake-specific, which is key for evaluating the validity of the SDT.

Q2: Are the Main Taxa of Primates Represented in Experimental Studies?

Experiments are constrained by the availability of the primate species kept in captivity or that can be easily observed in the field. We compared the primates involved in Non-SDT and SDT studies with the primates involved in Predation studies but also compared Non-SDT and SDT studies separately. Because humans are the most easily available primate species, it is likely that SDT and Non-SDT studies will rely primarily on human subjects.

Q3: Does Taxonomic Accuracy Differ Among Predator Types?

There is no practical reason for a difference in taxonomic accuracy between SDT, Non-SDT, and Predation studies. We thus quantified the taxonomic accuracy of the predators of primates in the three groups. We defined the taxonomic accuracy as the accuracy of the taxonomic allocation used to describe an animal and divided it into two groups (i.e., two taxonomic levels) to ensure a sufficient number of interactions in each group for statistical comparisons: 1) Species or Family; 2) Suborder or Order.

Statistical Analysis

For most analyses, we compared the occurrence of animals or items belonging to different categories across studies and within studies using contingency tables. Each experimental study (SDT and Non-SDT) can use a great variety of visual stimuli (e.g., snakes, flowers, objects) to examine the responses of different primate species while testing variable numbers of individuals. Some Predation studies can describe multiple predation events on primates, especially during long term monitoring of a group of primates. Consequently, the number of interactions (Ni) provides an

accurate measurement to quantify and compare, using robust statistical tests: 1) the distributions of primates tested versus observed, and 2) the stimuli used versus predators observed across the three groups of study. Thus, we decided to consider all interactions in the statistical analyses and to focus on Ni. Nonetheless, we also performed analyses using the number of publications (Np; Online Resource 1, Figs. 7–9). Because an experimental study could be included more than once when the experimenter(s) used different types of stimuli to test primate's reaction (generating pseudo-replicates), statistical tests were not conducted (selecting which type of stimulus per publication should be retained would have been arbitrary). Yet, we provided detailed information on the number of publications. We used Pearson's chisquare tests of independence to compare the distributions associated with each question under focus. For example, we only considered predator stimuli to compare the frequency of the main predators recorded in Predation studies versus the frequency of those used as picture or model stimuli in Non-SDT and SDT studies (Q1a). By contrast, we considered predator, non-predator animals and items to compare the distribution of stimuli used in Non-SDT and SDT studies (Q1b).

In addition to independence tests, we conducted chi-square tests of homogeneity to compare the distribution of stimuli used with a uniform distribution and pairwise chi-square comparisons using Bonferroni correction to adjust p-values for multiple comparisons to evaluate whether some types of stimuli were used preferentially. With the number of interactions per group and all statistical comparisons, we ranked stimuli groups from the most often to the least used and indicated the statistical differences with letters in the tables. Sample sizes varied depending on the question and the variable or category selected, so we indicated the number of interactions taken into account for each group in each test.

In independence tests, if the test was not applicable due to insufficient occurrences (less than 5 expected observations, Cochran, 1954), we excluded the group with the smallest expected frequencies from the contingency table. Consequently, the number of publications and interactions often differ slightly between those indicated in the statistical tests and those in the graphs. We performed post-hoc analyses based on residuals of Pearson's chi-squared test using Bonferroni correction to identify whether the observed frequency was significantly higher or lower than the expected frequency for each group.

For brevity, we presented only the main figures and summary tables. We performed all analyses using R (R Core Team, 2022) in the integrated development environment Rstudio (RStudio Team, 2022). We provide the database (Online Resource 3), publications reviewed (Online Resource 1, Table S2), bibliographic analysis grid (Online Resource 1, Table S3), details of the statistical analyses (Online Resource 1, Tables S4-S11), additional analyses with the number of publications as measurement (Online Resource 1, Figs. 7, 8, 9), and R script (Online Resource 4) in the electronic supplementary materials.

Ethical Note

No original data were collected for this study; thus, the matter of ethical approval does not arise.

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Data Availability Data and code are freely available in the electronic supplementary materials.

Results

Q1: Do Stimuli Used in Experimental Studies Include the Main Predators Encountered by Primates in the Wild?

a) Presence of the Main Predators of Primates in the Literature

The proportions of the main types of predators of primates observed in Predation studies, those used as stimuli in Non-SDT studies and those used as stimuli in SDT studies differed significantly (independence test:Ni = 4491;T = 2634.9 ~ χ_6^2 , p < 0.001; Table II). In Predation studies, most reported predation events involved primates, while interactions with raptors and carnivorans were observed less often, and those involving snakes and crocodilians were rare (Fig. 1). In Non-SDT studies, experimenters mostly presented primate and snake stimuli to primates, then carnivorans stimuli and rarely raptor and crocodilian stimuli (Fig. 1). In SDT studies, snakes were overwhelmingly common, raptors were not used, and few tests (i.e., interactions) involved a primate, a carnivoran, or a crocodile stimulus (Fig. 1). Raptors and primates were involved significantly more often in predation events (Predation studies) than used as predator stimuli in SDT and Non-SDT studies (Table II). Carnivorans were used significantly more often in Non-SDT studies than in predation reports and SDT studies (Table II). Snakes were used significantly more often in SDT studies than in Non-SDT studies and predation reports (Table II). Crocodiles were rare in Predation, SDT, and Non-SDT studies (Fig. 1; Table II). We found similar graphical results using Np as measurement (Online Resource 1, Fig. 7).

The considerable proportion of primate-on-primate predation events recorded (Fig. 1; Table II; Online Resource 1, Figs. 10 and 11) was mainly due to abundant predation

Table II Simplified results of Pearson's chi-square tests of independence and associated post-hoc tests comparing the main predators of primates in three types of study. "Predation" studies: predation events observed in natural conditions. "Non-SDT" studies: predator stimuli used in experimental studies that do not refer to the Snake Detection Theory (SDT). "SDT" studies: predator stimuli used in experimental studies framed around the SDT (Isbell, 2006)

Threat	Predation	Non-SDT	SDT
Raptor	+	_	_
Carnivorans	_	+	-
Snake	_	=	+
Primate	+	-	-
Crocodile	Е	Е	Е

"+" and "-" indicate the sign of the difference between the observed frequency and the expected frequency (z-score), positive or negative signs indicate a statistically significant difference (p < 0.05) and "=" indicates a nonstatistically significant difference (p > 0.05). "E" indicates a stimulus group excluded from Pearson's chi-squared test of independence



Fig. 1 Relative representation (% of interactions) of the main predators of primates in three types of studies. "Predation" studies: predation events observed in natural conditions. "Non-SDT" studies: predator stimuli used in experimental studies that do not refer to the Snake Detection Theory (SDT). "SDT" studies: predator stimuli used in experimental studies framed around the SDT (Isbell, 2006). "P" indicates the number of publications and "I" the number of interactions.

cases by chimpanzees (*Pan troglodytes*) reported notably in two publications (Stanford *et al.*, 1994; Watts & Amsler, 2013). Chimpanzees accounted for 98% of the primate-onprimate predation events with N=1,358 interactions over a total of N=1,381. Removing these outliers from the analyses drastically reduced the proportion of primate-on-primate predation events (5%), increased the prevalence of raptors (61%) and carnivorans (29%), and slightly changed the proportion of snake (3%) and crocodile predations (2%, Online Resource 1, Fig. 11). However, the main outcomes of pairwise comparisons did not change, showing that snakes were significantly more represented in SDT studies than in Predation studies and Non-SDT studies (Table II; Online Resource 1, Tables S4 and S5). In practice, removing chimpanzee predation events revealed that raptors and carnivorans are the main predators of primates in the wild.

b) Diversity of Stimuli Used in Non-SDT and SDT Studies

The visual stimuli presented to primates during experiments diverged markedly between Non-SDT and SDT studies (independence test,Ni = 7991;T = 762.9 ~ χ^2_{14} , p < 0.001). Primates, carnivorans, fish, and raptors were used more often as animal stimuli in Non-SDT studies than in SDT studies and snakes (although abundantly used) were not predominant (Fig. 2; Table III). The proportion of items was high both in SDT and

Non-SDT studies; objects and plants were used as controls and thus were used significantly more frequently than other stimuli (Table III). The difference of item frequency between SDT (39%) and Non-SDT (43%) might appear marginal in Fig. 2, but it was significant (Table III). In SDT studies, snakes were the most often used animal stimuli, all other taxa were poorly or not represented (Fig. 2; Table III). Regardless of the experimental study type, some stimuli were used preferentially in experimental studies (homogeneity test,Ni = 8035;T = 31062.0 ~ χ^2_{20} , p < 0.001), with snakes being the most often used animal stimuli due to their strong representation in SDT studies (Fig. 2; Table III). We found similar trends using Np instead of Ni (Online Resource 1, Fig. 8).

Q2: Are the Main Taxa of Primates Represented in Experimental Studies?

We found a significant difference between the preyed-on primate taxa in Predation studies and those tested in Non-SDT and SDT studies (independence test:Ni = 9816;T = 5893.6 ~ χ_6^2 , p < 0.001, Table IV). Most field observations of predation events concerned Afro-Eurasian monkeys (Fig. 3). By contrast, Non-SDT and SDT studies were highly biased toward apes (homogeneity test, Ni = 8035;T = 17875.4 ~ χ_3^2 , p < 0.001; Table IV; Online Resource 1, Fig. 12). We found similar trends using Np instead of Ni (Online Resource 1, Fig. 9). In experimental studies, the ape category was essentially represented by human subjects: 81% in SDT (N=4,311) and more than 99% in Non-SDT studies (N=2,863). Removing interactions with humans in experimental studies from the analyses drastically



Fig. 2 Relative representation of the stimuli in experimental studies. "Non-SDT" studies: predator stimuli used in experimental studies that do not refer to the Snake Detection Theory (SDT). "SDT" studies: predator stimuli used in experimental studies framed within the SDT (Isbell, 2006). "P" indicates the number of publications and "I" the number of interactions.

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Animal stimuli	Non-SDT	SDT	Statistical significance
Item	+	_	а
Snake	_	+	b
Primate	+	-	с
Arachnid	=	=	с
Other Mammalia	_	+	d
Bird	_	+	d,e
Carnivorans	+	-	e,f
Insect	=	=	f
Amphibian	_	+	g
Fish	+	-	h
Lizard	_	+	i
Na	_	+	i,j
Mollusc	_	+	j,k
Cnidaria	_	+	j,k,l
Raptor	+	-	k,l
Worm	Е	Е	1
Crocodile	Е	Е	l,m
Tortoise	Е	Е	l,m
Marsupial	Е	Е	1,m
Dinosaur	Е	Е	m
Crustacea	Е	Е	m

"+" and "-" indicate the sign of the difference between the observed frequency and the expected frequency (z-score), positive or negative signs indicate a statistically significant difference (p < 0.05) and "=" indicates a non-statistically significant difference (p > 0.05). Stimulus groups sharing the same letter in the "Statistical significance" column are not statistically different from each other (p > 0.05), based on pairwise chi-square comparisons. "E" indicates a stimulus group excluded from the Pearson's chi-squared test of independence

reduced the proportion of apes in Non-SDT studies (4%) and in SDT studies (56%), increased the prevalence of Afro-Eurasian monkeys in Non-SDT studies (72%) and in SDT studies (40%), and slightly changed the proportion of Pan-American monkeys in Non-SDT studies (21%, Online Resource 1, Fig. 13). However, the main outcomes of pairwise comparisons did not change. Apes were significantly more represented in SDT than in Predation studies and Non-SDT studies. This difference was due to one SDT study using pictures of snakes to test the disruptive effect of negative stimuli on the cognitive abilities of chimpanzees, gorillas, and Japanese macaques (Hopper *et al.*, 2021; Table IV; Online Resource 1, Table S8). More

Table III Simplified results of Pearson's chi-square tests of independence and associated post-hoc tests comparing the stimuli used in experimental studies. "Non-SDT" studies: predator stimuli used in experimental studies that do not refer to the Snake Detection Theory (SDT). "SDT" studies: predator stimuli used in experimental studies framed around the SDT (Isbell, 2006)

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Table IV Simplified results of Pearson's chi-square tests of independence and associated post-hoc tests comparing the primate taxa represented in the three types of study. Simplified results of the chi-square test of homogeneity and associated post-hoc tests comparing the primate taxa represented in SDT and Non-SDT studies. "Predation" studies: predation events observed in natural conditions. "Non-SDT" studies: predator stimuli used in experimental studies that do not refer to the Snake Detection Theory (SDT). "SDT" studies: predator stimuli used in experimental studies framed around the SDT (Isbell, 2006)

Broad taxon	Predation	Non-SDT	SDT	Statistical significance
Apes	_	+	+	а
Afro-Eurasian monkeys	+	_	-	b
Pan-American monkeys	+	_	-	с
Strepsirrhines & Tarsiiformes	+	-	-	d

"+" and "-" indicate the sign of the difference between the observed frequency and the expected frequency (z-score), positive or negative signs indicate a statistically significant difference (p < 0.05). Stimulus groups sharing the same letter in the "Statistical significance" column are not statistically different from each other (p > 0.05), based on pairwise chi-square comparisons and chi-square test of homogeneity for SDT and Non-SDT studies only

importantly, whatever the case, in experimental studies, Pan-American monkeys were underrepresented (especially in SDT studies), whereas Strepsirrhines and Tarsiiformes were absent.



Fig.3 Relative representation (% of interactions) of the primate taxa in three types of studies. "Predation" studies: predation events observed in natural conditions. "Non-SDT" studies: predator stimuli used in experimental studies that do not refer to the Snake Detection Theory (SDT). "SDT" studies: predator stimuli used in experimental studies framed around the SDT (Isbell, 2006). "P" indicates the number of publications and "T" the number of interactions.



Fig. 4 Relative representation (% of interactions) of predators identified to species or family *versus* suborder or order in three types of study. "Predation" studies: predation events observed in natural conditions. "Non-SDT" studies: predator stimuli used in experimental studies that do not refer to the Snake Detection Theory (SDT). "SDT" studies: predator stimuli used in experimental studies framed within the SDT (Isbell, 2006). "P" indicates the number of publications and "I" the number of interactions.

Q3: Does Taxonomic Accuracy Differ Among Predator Types?

Predators in SDT and Non-SDT studies were not identified as accurately as in Predation studies (independence test: Ni = 4509;T = 1689.3 ~ χ_2^2 , p < 0.001; Fig. 4; Table V). In SDT and Non-SDT studies, snakes were often crudely identified compared with other predators (independence test:Ni = 2728;T = 1496.8 ~ χ_4^2 , p < 0.001; Table VI). Snake stimuli were named more accurately in Non-SDT studies than in SDT studies (independence test:Ni = 1774;T = 12.9 ~ χ_1^2 , p < 0.001; Table VII).

Table V Simplified results of Pearson's chi-square tests of independence and associated post-hoc tests comparing the taxonomic accuracy of predators between groups of study. "Predation" studies: predation events observed in natural conditions. "Non-SDT" studies: predator stimuli used in experimental studies that do not refer to the Snake Detection Theory (SDT). "SDT" studies: predator stimuli used in experimental studies framed around the SDT (Isbell, 2006)

Taxonomic accuracy	Predation	Non-SDT	SDT
Species or Family	+	=	_
Suborder or Order	-	=	+

"+" and "-" indicate the sign of the difference between the observed frequency and the expected frequency (z-score), positive or negative signs indicate a statistically significant difference (p < 0.05) and "=" indicates a non-statistically significant difference (p > 0.05)

Table VI Simplified results of Pearson's chi-square tests of independence and associated post-hoc tests comparing the taxonomic accuracy between predators used in experimental studies	Taxonomic accuracy	Species or Family	Suborder or Order
	Raptor Carnivorans	+ +	_
	Snake	_	+
	Crocodile	=	=
	Primate	+	-

"+" and "-" indicate the sign of the difference between the observed frequency and the expected frequency (z-score), positive or negative signs indicate a statistically significant difference (p < 0.05) and "=" indicates a non-statistically significant difference (p > 0.05)

Table VII Simplified results of Pearson's chi-square tests of independence and associated post-hoc tests comparing the taxonomic accuracy of snake stimuli in experimental studies. "Non-SDT" studies: predator stimuli used in experimental studies that do not refer to the Snake Detection Theory (SDT). "SDT" studies: predator stimuli used in experimental studies framed around the SDT (Isbell, 2006)

Taxonomic accuracy	Non-SDT	SDT
Species or Family	+	_
Suborder or Order	_	+

"+" and "-" indicate the sign of the difference between the observed frequency and the expected frequency (z-score), positive or negative signs indicate a statistically significant difference (p < 0.05)

Discussion

Comparisons among publications related to predation events recorded in the wild, Non-SDT, and SDT experimental studies highlighted strong biases. The primate species tested in experimental studies and the predator stimuli used to elicit responses did not coincide with the range of primate-predator interactions observed in the wild. This mismatch was strong and key stimuli and primate species were lacking in the experimental SDT studies. Moreover, both the stimuli and the primate species selected in SDT studies markedly differed from those used in Non-SDT studies.

Predator Diversity Bias

Analyses indicated that reports of predation events on primates observed in the wild failed to support the assumption that snakes are major predators of modern primates. Instead, raptors, carnivorans, and to a lesser extent other primates (when chimpanzee studies are discarded, Online Resource 1, Fig. 11) exert strong predatory pressures on primates, a result supported by extensive reviews of primate ecology (Ferrari, 2009; Fichtel, 2012; Goodman *et al.*, 1993; Mittermeier *et al.*, 2013). Although the conclusions that can be drawn are limited due to the difficulty of witnessing predation events on primates, it still seems unlikely that the low observed predation rate by snakes compared to other predator types might result from an underestimation.

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Raptors were involved in numerous predation events on primates observed in the field but were strongly underrepresented or absent in experimental studies. Carnivorans also provided many cases of predation; they were slightly overrepresented in Non-SDT studies and strongly underrepresented in SDT studies. Snakes were very rarely involved in wild predation events but were frequently used in Non-SDT studies and overwhelmingly used in SDT studies. This rarity of observed predation attempts cannot be explained by the secretiveness of snakes. While raptors kill their prey and take away their catch rapidly, snakes swallow their prey slowly, just after the catch, especially large items, increasing the observation probability. Raptors are used as audio stimuli in primate, antipredator experimental studies (Fichtel, 2007; Fichtel & Kappeler, 2002). The inclusion of audio stimuli in our data would have likely increased the number of raptors used in experimental studies. However, primates use both acoustic and visual clues in search of raptorial threats (Gil-da-Costa *et al.*, 2003; Westoll *et al.*, 2003). There was even less reason for their absence as visual stimuli in SDT studies (Mcgraw & Berger, 2013).

Surprisingly, primate-on-primate predation provided more than three quarters of the predation events recorded in the field, surpassing raptors and carnivorans. Most cases involved chimpanzees predating monkeys (76%, N = 1,358 among 1,781 events), especially red colobus monkeys (Piliocolobus sp.). This overrepresentation was due to very large samples (N>300 events) provided by few field studies where groups of habituated chimpanzees were closely monitored during specialized hunting, with a huge amount of data amassed over time (Stanford et al., 1994; Watts & Amsler, 2013). In contrast, in most reports of predation on primates (other predators than chimpanzees), sample sizes were small and often limited to a single observation (e.g., 1 monkey killed by a felid). By excluding chimpanzee predation studies, 5% of the total predation events involved another primate (N=23); then raptors and carnivorans are the main predators of primates, representing respectively 61% and 29% of the total number of predation events recorded in the field (Online Resource 1, Fig. 11). Chimpanzees are certainly a predatory threat to smaller primates (Boesch & Boesch, 1989; Gašperšič & Pruetz, 2004; Newton-Fisher et al., 2002; Wrangham & Riss, 1990), but field evidences show that primates in general are predators of primates (Butynski, 1982; Cheney et al., 1981; Hohmann & Fruth, 2007; Jolly et al., 2000; Utami & Van Hooff, 1997).

Crocodilians were poorly represented in our data. This result was unexpected, because numerous reports show that crocodiles are a major threat to humans (Das & Jana, 2017; Fukuda *et al.*, 2014; García-Grajales & Buenrostro-Silva, 2019; Wallace *et al.*, 2012). They would have been well represented if our literature survey had included nonscientific reports (e.g., many cases have been published in local newspapers) and had focused on predation of humans by large predators. Nonetheless, the low occurrence of crocodiles is not easy to explain. The extreme rapidity of crocodilian attacks may have reduced observation opportunities. Whatever the explanation, the low occurrence of crocodiles in experimental studies does not allow us to determine whether these large predators trigger a strong fear and antipredator response and this issue deserves further investigation.

Considering all types of stimuli used in experimental studies, including various animals (predators, herbivores, etc.), plants and objects used as control stimuli,

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Non-SDT studies mainly used primates and then carnivorans (Fig. 2). Many domestic objects and a wide variety of plants were used as visual control stimuli, making this group the largest type of stimuli used. This suggests that experimenters incorporated a wide variety of items as control stimuli in their tests but did not do the same with predators. Snakes were the most often used animal stimuli in SDT studies. Most SDT studies compared the reactions of humans facing snakes, various objects, or harmless animals, such as spiders (Hauke & Herzig, 2017), but neglected other major predators. The discrepancy between the predators of primates observed in the wild and the stimuli used in SDT experiments makes it difficult to assess comprehensively the main predictions of the SDT. Our results question the legitimacy of focusing almost exclusively on snakes as evolutionary-relevant stimuli when studying the influence of predators on primate evolution. Instead, we believe that observed predation events should provide a baseline for the design of experimental studies.

Primate Diversity Bias

The diversity of primates facing predation in the wild did not coincide with the species involved in Non-SDT and SDT studies. Predation observations involved a wide range of primate species in the field, but experimental studies most often tested apes, almost exclusively humans, and to a lesser extent included Afro-Eurasian monkeys. Pan-American monkeys were largely neglected, whereas Strepsirrhines and Tarsiiformes were totally overlooked. This may partly result from observational difficulties: arboreal and nocturnal primates are not easily observed. However, many primate taxa would make suitable subjects in captive conditions. Focusing on nonhuman primates inevitably increased taxonomic diversity of the subjects tested in experimental studies (Fig. 3, Online Resource 1, Fig. 13). Despite a general taxonomic bias in primate cognition studies and in field primatology in general (Altschul et al., 2019; Bezanson & McNamara, 2019), the almost exclusive focus of experimental studies on humans and on a handful of macaques results from the choice of experimenters. This choice may echo the appealing idea that the SDT provides a straightforward explanation for snake phobia (e.g. National Geographic News, 2017), possibly prompting studies looking for the fear module dedicated to snakes in the human brain (Kawai, 2019). According to the SDT, Pan-American monkeys, Strepsirrhines and Tarsiiformes should exhibit lower abilities to detect snakes compared to Afro-Eurasian monkeys and apes. Unfortunately, the rarity or absence of tests performed with representatives of these main taxa precludes comparison across primate species.

Taxonomic Accuracy Bias

The taxonomic status of the predators of primates was reported less accurately in experimental than in field studies. This bias resulted almost exclusively from the low taxonomic accuracy used to describe snake stimuli in experimental studies. Snakes were well described in field predation studies, and they were described more precisely in Non-SDT studies than in SDT studies. This dearth of taxonomic accuracy

is not justified by technical difficulties because pictures and scientific names are available for almost all snake species.

The SDT distinguishes between rapid visual detection and slower visual-cognitive recognition; investigators focusing on the former may see no reason to consider specific snake species, because they presumably all share visual cues unique to snakes that allow for rapid detection and processing of emotionally significant information by primates (Isbell & Etting, 2017; Lobue & Deloache, 2011; Van Strien & Isbell, 2017). If a snake shape represents a serious threat, it is logical to assume that strong selection occurred for an innate general detection mechanism for all snakelike stimuli (Bertels et al., 2020; Ohman & Mineka, 2001). However, whether for rapid detection or slower recognition experiments, the deficiency of tests with primates facing different snake species is regrettable because more than 3,900 species of snakes have been inventoried. Snakes exhibit an immense variety of body sizes, body shapes, and colour patterns (Allen et al., 2013). Some primates can differentiate dangerous from harmless snakes (e.g., moor macaques, Macaca maura; Hernández Tienda et al., 2021) and behave accordingly (Falótico et al., 2018). Besides, an encounter may be risky for the primate (Adukauskiene *et al.*, 2011; Foerster, 2008; Shine et al., 1998), but it also may be risky for the snake, including venomous species (Boinski, 1988; Da Silva et al., 2019; Lorenz, 1971). Large, potentially dangerous snakes have evolved an extended repertoire of warning signals to avoid confrontation and minimize the use of defensive strikes (Glaudas & Winne, 2007).

Primate–snake relationships are likely more complex than assumed in most experiments reviewed in this study. To demonstrate that snakes elicit particular responses in primates, irrespective of the snake's appearance, it is crucial to account for the diversity of snakes. Therefore, the taxonomic accuracy of the visual stimuli used in experiments should be improved and investigators should compare reactions of different primate species facing a wide range of snake species encompassing sizes, colour, body shapes, and behaviours.

Limitations and Caveats

Many limitations of our survey could not be considered, such as the difficulty of encompassing the diversity of predation reports. We performed a systematic search and adopted automatic procedures to select scientific articles that excluded numerous reports of predation events on primates published in non-scientific journals (i.e., newspaper articles). Another difficulty emerged from the lack of standardization in the methodology and approaches used in field and experimental studies. Some reports involved a single predator, a single prey, and a single event; other studies were based on a wide diversity of stimuli, including different primate subjects and a range of tests. Despite this disparity, results obtained using Np were similar to those using Ni, suggesting that our conclusions are robust.

Other limitations could not be considered. For example, observational biases affect which predation events can be recorded in the field. Technical difficulties to present realistic stimuli to the primates tested also limit our ability to measure their responses in a relevant manner. In addition, the proxies used to assess the fear

response of animals (including humans) often are indirect (e.g., pupil dilatation) and not easy to interpret.

Nonetheless, the strong methodological biases we found in experimental studies are based on a large data set and on different albeit complementary questions. All the results converge to highlight a mismatch between laboratory and ecological evidences. They cannot be explained by observational difficulties in the field or other limitations evoked above. Instead, they largely resulted from the choice of the experimenters.

Conclusions

Abundant ecological evidence shows that predation attempts on modern primates are largely exerted by other animals than snakes. Yet, by heavily focusing on snakes and neglecting the role of carnivorans and raptors in the evolution of primate traits (Isbell, 2006, 2009; Kawai, 2019), SDT-related studies are unable to determine whether fear responses are snake-specific or anti-predator more generally. The biases we show here suggest that studies focusing on predator detection might benefit from including a more comprehensive list of predators and primates and should focus on phylogenetic gaps in the primates tested.

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Declarations

Conflict of Interest The authors declare that they have no conflict of interest.

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ORIGINAL RESEARCH

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No evidence for female kin association, indications for extragroup paternity, and sex-biased dispersal patterns in wild western gorillas

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Abstract

Characterizing animal dispersal patterns and the rational behind individuals' transfer choices is a long-standing question of interest in evolutionary biology. In wild western gorillas (Gorilla gorilla), a one-male polygynous species, previous genetic findings suggested that, when dispersing, females might favor groups with female kin to promote cooperation, resulting in higher-than-expected within-group female relatedness. The extent of male dispersal remains unclear with studies showing conflicting results. To investigate male and female dispersal patterns and extragroup paternity, we analyzed long-term field observations, including female spatial proximity data, together with genetic data (10 autosomal microsatellites) on individuals from a unique set of four habituated western gorilla groups, and four additional extragroup males (49 individuals in total). The majority of offspring (25 of 27) were sired by the group male. For two offspring, evidence for extragroup paternity was found. Contrarily to previous findings, adult females were not significantly more related within groups than across groups. Consistently, adult female relatedness within groups did not correlate with their spatial proximity inferred from behavioral data. Adult females were similarly related to adult males from their group than from other groups. Using R_{sT} statistics, we found significant genetic structure and a pattern of isolation by distance, indicating limited dispersal in this species. Comparing relatedness among females and among

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males revealed that males disperse farer than females, as expected in a polygamous species. Our study on habituated western gorillas shed light on the dispersal dynamics and reproductive behavior of this polygynous species and challenge some of the previous results based on unhabituated groups.

KEYWORDS

dispersal, great apes, kin association, paternity, polygynous species, western gorillas

1 | INTRODUCTION

Sociality, the persistent affiliative association of individuals in groups observed in some animal species, is thought to have evolved for different reasons, one of which is to promote cooperation among kin (e.g., Van Horn et al., 2004). However, even though cooperative behaviors are usually beneficial for individuals (Silk, 2007), the grouping of close relatives can also lead to inbreeding, resulting in high fitness costs (Keller & Waller, 2002; Lukas & Clutton-Brock, 2011; Pusey & Wolf, 1996). Thus, many species have developed specific behaviors and mating strategies to avoid inbreeding, such as the exclusive or majority dispersal of one sex. In social mammals, male-biased dispersal is the most commonly observed pattern (Greenwood, 1980; Lawson Handley & Perrin, 2007), as it prevents mating between related individuals while allowing female kin to stay together and cooperate (Kin selection theory: Hamilton, 1964; Silk, 2007). In some mammal species (e.g., equids, bats, primates: Clutton-Brock & Lukas, 2012), including gorillas (Gorilla spp.), natal dispersal (before reproduction) occurs in both sexes. This allows females to avoid mating with their father and brothers (Clutton-Brock, 1989), and reduces feeding competition by limiting group size (Crockett & Janson, 2000; Vick & Pereira, 1989). In such cases with both male and female dispersal, cooperation between females is rare and female commonly disperse again after natal dispersal (secondary dispersal), as shown, for example, in bats (Debeffe et al., 2015), equids (Nagy et al., 2007), and gorillas (Robbins & Robbins, 2015; Stokes et al., 2003).

While both sexes disperse in the genus *Gorilla*, the two species present different social strategies (Harcourt & Stewart, 2007a; Robbins & Robbins, 2018). Breeding groups of western gorillas (*G. gorilla*) typically include one silverback (Breuer et al., 2010; Gatti et al., 2004; Parnell, 2002), while in eastern gorillas (*G. beringei*), for the well-studied mountain gorilla, multiple males frequently coexist in a single group (40% of the groups), even though a dominant silverback sires most of the offspring (Bradley et al., 2005). The twice more frequent secondary female dispersal found in western versus eastern gorillas might thus be explained by the greater need of western gorilla females to increase mate choice and reproductive success (Baudouin et al., 2019; Manguette, Robbins et al., 2020; Stokes et al., 2003).

Additionally, western gorillas are seasonal frugivores (Doran et al., 2002; Doran-Sheehy et al., 2009; Masi et al., 2009) and thus are likely to experience higher feeding competition than the mainly folivorous mountain gorillas. Reliance on monopolizable resources such as fruit may indeed reduce the advantage of cooperative behaviors between females (Wrangham, 1980).

In a mountain gorilla population, a pattern of isolation by distance (i.e., a positive correlation between genetic and geographic distances) was observed for females but not for males, suggesting a larger mean dispersal distance for males than for females (Roy et al., 2014). In western gorillas, conflicting genetic results were reported on male dispersal patterns. One study identified genetic networks among males (with males being more related to neighboring males than to distant ones) (Bradley et al., 2004), advocating for limited male dispersal. However, two other studies, both at similar and larger geographical scale (6,000 km² compared to the previously mentioned study of 30 km²), found a single undifferentiated population based on Y-chromosome microsatellite markers, thus consistent with extensive male dispersal (Douadi et al., 2007; Inoue et al., 2013).

For females, natal dispersal always occurs before the first reproductive event; secondary dispersal can occur soon after that or later in their reproductive life (Manguette, Robbins et al., 2020; Stokes et al., 2003). Previous studies suggested females immigrate preferentially into smaller breeding groups, selecting nascent units with younger and stronger silverbacks to avoid feeding competition and disease, and/or to increase protection and reduce attraction by infanticidal males or predators (Manguette, Robbins et al., 2020; Stokes et al., 2003). Transfers depend on various factors, including group size, group age, male phenotypic traits such as crest size (Baudouin et al., 2019; Breuer et al., 2012; Manguette, Robbins et al., 2020; Stokes et al., 2003) and loss of infants (Bai Hokou, longterm data). In mountain gorillas, female relationships are clearly stronger among related females than among nonrelated females of the same group (Watts, 1994). If kin associations are also important in western gorillas, it could be hypothesized that female dispersal preserves these associations, either through single female dispersals toward groups that include related females or through co-transfer of related females to the same group. Indeed, multifemale transfers between groups have been documented during both natal and secondary dispersals in western gorillas (Manguette et al., 2020; Stokes et al., 2003). At the same time, females are expected to avoid groups led by related males, in order to avoid consanguinity (Bradley et al., 2007).

Bradley et al. (2007) tested the hypothesis of female gorillas favoring groups with female kin in unhabituated groups and found that the average within-group relatedness among females was higher FIGURE 1 Spatial distribution of the study groups, with the group compositions of sampled individuals. CAR1/CAR2 are groups sampled at two field sites in Central African Republic (CAR), and RC1/RC2 are groups sampled at one field site in Republic of Congo (RC). The number of individuals sampled in each group is written in parenthesis (note that one individual from RC1 did not produce enough genetic data so was removed from the dataset for the genetic analyses). Pop. Population; SB, Silverbacks; AF, Adult Females; IM, Immatures, this includes all offspring from each study group, thus young silverbacks, blackbacks, subadults, juveniles and infants; Other SB, corresponds to two solitary silverbacks and two silverbacks from semi-habituated groups



than expected under a model of random dispersal. This result suggested that female kin associations occur during transfers or that females preferentially disperse to groups with female kin (Arandjelovic et al., 2014; Douadi et al., 2007). In parallel, the authors also found that the average relatedness of females to their group silverback was lower than expected, advocating the hypothesis that females avoid related males when dispersing. In mountain gorillas, it has been observed that female pairs are on average genetically more related within groups than among groups, yet male-female pairs were counter-intuitively found to be genetically more related within groups than among groups (Roy et al., 2014). In western gorillas, the higher-than-expected level of female relatedness within groups inferred by Bradley et al.'s (2007) and Arandjelovic et al.'s (2014) study contrasts not only with other studies (Douadi et al., 2007; Inoue et al. 2013) but also with field observations that show very few social interactions among females or adults in general, either affiliative or even competitive (Doran-Sheehy et al., 2009; Stokes, 2004; Masi 2020). Grooming and other physical affiliative behaviors have not been much recorded among wild western gorilla adults (Masi et al., 2009; Masi, 2020), raising the question of whether adult females have or not inclusive fitness benefits to having close kin in the same group.

Importantly, given the difficulties of habituating western gorillas (Doran-Sheehy et al., 2007), all previous genetic studies in this species were based on fecal samples of unidentified individuals collected at nest sites (Arandjelovic et al., 2014; Bradley et al., 2007; Douadi et al., 2007). However, doing so results in potential individual misidentification, in particular in misidentifying predispersal subadult females as adult females. Moreover, all group members will not necessarily be sampled, which can result in higher or lower average relatedness by chance or sampling bias. These biases are particularly problematic when investigating within-group female relatedness. Indeed, it is very difficult to know, from nest data alone, whether a female is an adult or a predispersal adolescent female, given that their body and dung size are roughly the same; and a predispersal adolescent female will inherently be strongly related to at least another group female, if her mother is still present. To get around this, some studies (Arandjelovic et al., 2014; Bradley et al., 2004) have combined multiple criteria, such as dung size, additional presence of infant feces in the nest, and absence of genetic relatedness with the silverback.

Here we analyzed, for the first time, genetic data from several groups of western gorillas (*G. gorilla*) in Central Africa. The study groups were habituated, providing the opportunity to identify with certainty the age/sex classes of dung samples, to sample nearly exhaustively all individuals, as well as to compare genetic data with behavioral observations and to make inferences about an individual's putative parents.

To investigate relatedness between males and females within and among groups ranging at different distances from each other, we collected fecal samples from 50 individuals in an area of approximately 110 km² spread over a maximum distance of 70 km (Figure 1). Specifically, we investigated whether adult breeding females are (a) more related to within-group females than those from other groups to favor cooperation (as suggested by Arandjelovic et al., 2014; Bradley et al., 2007) and (b) less related to their group silverback than to other silverbacks to limit inbreeding (as suggested by Bradley et al., 2007). We then investigated whether genetic relatedness influenced withingroup affiliative behavior among adult females (measured by spatial proximity), since kinship frequently coincides with proximity patterns and affiliative behavior (e.g., Kapsalis & Berman, 1996). Last, we compared genetic differentiation in males and females in relation to their geographic proximity. We expected males to disperse over greater distances, given that, unlike females, male gorillas spend at least part of their life history ranging as solitary individuals in search of (unrelated) females (Breuer et al., 2010; Parnell, 2002). This is expected to result in less genetic structure than for females within the same geographic area (Douadi et al., 2007; Roy et al., 2014). Investigating sex-specific spatial genetic structure is crucial to increase our understanding of dispersal dynamics of the species.

2 | METHODS

2.1 | Study site, sample, and behavioral data collection

Our study was carried out at three field sites within the Sangha Trinational protected area complex (https://whc.unesco.org/en/ list/1380): (a) Bai Hokou (N 2° 51.574', E 16° 28.045'; Datum: WGS84), (b) Mongambe (N 2° 55.077'; E 16° 23.324', Datum: WGS84) in Dzanga-Ndoki National Park (DNNP, 1,222 km²) in the southwestern part of the Central African Republic (CAR), and (c) Mondika (N 4° 39.000'; E 18° 56.000', Datum: WGS84) in the Djeke Triangle west of Nouabalé-Ndoki National Park in the Republic of Congo (RC) bordering DNNP. The distance between Bai Hokou and Mongambe in CAR and Mondika is approximately 57 and 61 km, respectively, across contiguous forest. The Sangha Trinational largely consists of semi-deciduous rainforest (Harris, 2002) with a seasonal climate and a dry season (<100 mm monthly rainfall) between December and February and a peak rainy season between September and October.

We collected fecal samples from 50 individuals, of which 46 belonged to four habituated groups of western gorillas: 14 individuals from one group at Bai Hokou (named CAR1), 11 individuals from one group at Mongambe (CAR2), and 12 and 9 individuals, respectively, from two groups at Mondika (RC1 and RC2) (Figure 1). The two habituated groups in CAR were 9.1 km apart, and the two RC habituated groups had overlapping home ranges (Figure 1). We therefore sampled 46 individuals out of the 54 who composed the study groups throughout the study period. Samples from CAR1 group were collected between 2008 and 2017, those from CAR2 between 2011 and 2017, while samples from both RC groups were collected in 2014. During these study periods, we recorded the date and the identity of immigrant and emigrant individuals. The group composition changed over time mostly in terms of offspring or dispersing individuals, but little changes occurred in terms of acquisition of new adult females who then reproduced in the groups (one female and two females acquired in CAR-1 and RC-1 groups, respectively). The study group compositions are indicated in Figure 1 for the sampled individuals and in Table S1 for all individuals. We used age classes from Breuer et al. (2009).

To increase the adult male sample size (given western gorillas' one-male social system), we also sampled, between 2008 and 2017, the fecal samples of two silverbacks from two semi-habituated groups and two unhabituated solitary silverbacks within the home range of two CAR habituated groups. The home range of the two silverbacks from the semi-habituated groups (SB1 and SB2) partially overlapped with those of CAR1 and CAR2, respectively, while the two solitary silverbacks (LSB1 and LSB2) ranged within the home range of CAR1 and SB1 (Figure 1). Fecal samples were collected by

Sh.M., T.F., and E.M. from identified individuals immediately after defecation during continuous focal follows (Altmann, 1974) and preserved in the field via the two-step method (ethanol-silica gel as described in (Arandjelovic et al., 2009).

Behavioral data collection included half-day and full-day observations of adult females between April to June 2008, June to August 2017, and June to July 2019 for the CAR groups, and April to May 2014 for the RC groups (female focal follows: N = 46 days and N = 11,536 total min; N = 520 scans with female-female distance). Behavioral data for this study were collected only in the frugivory season (see Masi et al., 2009, 2015 for seasonal definition) to control for variation in interindividual distances in relation to changes in fruit availability (Masi et al., 2009). Spatial proximity data among the adult females of each of the four habituated groups were collected by Sh.M., A.S.M., and S.M. for CAR groups, and A.S.G. and E.M. for RC groups (hours of focal sampling per each adult female dyad are provided in Table S2). The distance of the focal adult female to any other visible adult females of the group was collected using instantaneous scan sampling at 10-min intervals (Altmann, 1974); for methods see (Masi & Breuer, 2018; Masi et al., 2009, 2012). For each scan, the distance was recorded according to three spatial categories: 0-5m, 6-10 m, and ≥10 m. If in a scan, the distance from the nonfocal female was not recorded, a distance of more than >10 m was assigned.

Western gorillas are listed as critically endangered by IUCN, and all samples were collected noninvasively under governmental authorization by Ministries of Education and Water and Forests of the CAR government and the Ministry of Scientific Research and Ministry of Forest Economy of RC. This research adhered to ethics and healthy protocols and legal requirements of the governments of both CAR and RC. All applicable international, national, and/or institutional guidelines for the care and use of animals were followed.

2.2 | Geographic distance between the study groups

Geographical distances between the different study groups were calculated using the GPS coordinates of the center point of each habituated group's home range, which in turn were determined from long-term data of each group's ranging patterns (2–4 years depending on the study group). Since the fecal samples of the two lone silverbacks and the two semi-habituated silverbacks were collected within the home range of either the CAR1 or the CAR2 group (see Figure 1), we used the coordinates of the corresponding group for these silverbacks. CAR and RC groups belonged to a continuous population spread across those two countries, and no geographic barriers were present between them.

2.3 | DNA extraction and genotype

Genomic DNA was extracted from 60 fecal samples, corresponding to 50 individuals (five individuals were extracted twice, using an additional fecal sample, due to poor quality data from the first extraction; and five fecal samples corresponded to already typed individuals). We used the QIAamp PowerFecal DNA kit (QIAGEN, USA), with approximately 100mg of fecal material. Based on previous literature (Arandjelovic et al., 2009, 2011; Bradley et al., 2000; Fünfstück et al., 2014; Roy et al., 2014), we chose 10 autosomal microsatellite loci (D2s1326, D4s1627, D5s1470, D6s1056, D7s817, D8s1106, D10s1432, D14s306, D16s2624, vWF), in addition to the amelogenin locus to identify the sex. We modified three primers in order to better match the gorilla genome (see Table S3). PCR amplifications were performed in a final volume of 20 µl composed of 0.5 U of Taq polymerase, 125 nM of each primer, 200 μ M of dNTPs, $1\times$ of buffer, and 1μ l of extracted DNA. The reactions were performed in an Eppendorf Mastercycler with an initial denaturation step at 94°C for 5 min, followed by 36 cycles at 94°C for 30 s, 55°C for 30 s. 72°C for 20 s. and a final extension of 72°C for 10 min. Loci genotyping was realized with two sequencing multiplexes of six and five STRs, respectively (Table S3). Each genotype was obtained from at least three independent PCRs. Forward primers were fluorescently labeled, and reactions were further analyzed by capillary electrophoresis (ABI 310, Applied Biosystems). We used the software package GeneMarker (SoftGenetics LLC) to obtain allele sizes from the PCR product analysis. We chose to keep all individuals with more than six valid STRs, resulting in the removal of one individual (in the RC1 group). We thus had a final dataset of 49 individuals, corresponding to 22 adults and 27 infants/juveniles (i.e., one immature was removed).

2.4 | Genetic inferences of parent-offspring relationships

We genetically assessed the parent-offspring relationships of every immature present in the samples using two methods, Cervus 3.0.7 (Kalinowski et al., 2007) and RELPAIR 2.0.1 (Epstein et al., 2000), in order to assess these relationships with more certainty. We also investigated this relationship for an adult female (RC1-F4), who transferred from the RC2 group into the RC1 group while under observation. RELPAIR uses a maximum likelihood method according to the allele frequencies in the population that looks separately for maternities and paternities. We chose to run this software including all adults and each offspring, one by one, as well as including adults only, and we retained all relationships that came out as significant with a likelihood ratio higher than 10. For Cervus, we performed first a parentage analysis aiming at inferring jointly the father and mother of offspring, considering all adult females as potential mothers and all adult males as potential fathers. Separate paternity and maternity analyses were then performed for the offspring for which both parents could not be jointly identified. We assumed that 50% of candidate parents had been sampled and used a typing error rate of 1%, with 80% and 95% for relaxed and strict level of confidence, respectively. Confidence levels were computed based on the likelihood scores, using the standard simulation procedure developed in

Cervus. We recorded also the number of mismatches between parents and offspring in each case.

2.5 | Calculation of relatedness estimators and population differentiation among adults

We calculated two estimators of relatedness: QG (Queller & Goodnight, 1989) and LR (Lynch & Ritland, 1999), which are both method-of-moment estimators and perform better with data including five to twenty STRs (Csilléry et al., 2006). We used Kingroup (Konovalov et al., 2004) to calculate these estimators between all pairs of adult individuals and their associated p-values (obtained by reshuffling sample alleles at each locus). In addition, we also estimated a kinship coefficient among all pairs of adult individuals using the Loiselle estimator (Loiselle et al., 1995), as implemented in SpaGeDi 1.5d (Hardy & Vekemans, 2002). Using the permutation analysis procedure implemented in the function grouprel of the related R package available at https://github.com/timothyfrasier/ related, we determined whether females were significantly more related within each of the four groups than across groups. We then grouped all individuals by country (RC versus CAR) and assessed separately for males and females whether they were significantly more related within each country than among them. We determined also whether females were significantly more related to their silverback than to the other males in the population, using our own R script. We performed 10,000 permutations in each case.

We also estimated fixation indices among populations to determine the genetic structure of the different groups. We first grouped the two RC populations and the two CAR populations, respectively, and calculated a $R_{\rm ST}$ between countries, knowing that this index is specifically designed for microsatellite markers (Slatkin, 1995). We tested whether the R_{sT} significantly differed from zero by performing 10,000 permutations of individuals among all populations. Then, we computed all pairwise R_{ST} values between all four groups and regressed the pairwise values of R_{sT} $(1-R_{sT})$ against the logarithm of the distance. A positive regression slope is expected under a two-dimensional isolation-by-distance (IBD) model (i.e., the greater the geographical distance, the higher the genetic distance; Rousset, 1997). The significance level of this slope was assessed by performing 10,000 permutations of population locations among all populations, which is equivalent to a Mantel test. All R_{sT} analyses were performed with SpaGeDi 1.5d, considering either all adult individuals or all adult females only. We could not perform the analyses on all adult male individuals, as there were only eight male individuals in total, with two groups containing only one male individual.

3 | RESULTS

We successfully obtained genotypes at 10 microsatellites for 49 out of the 50 sampled western gorillas: 45 individuals belonging to four habituated groups, two silverbacks from semi-habituated groups, and two lone silverbacks (Figure 1). All pairs of individuals had at least five markers in common. The 10 microsatellites had an average number of alleles of 6.8, with an average heterozygosity $H_{\rm e}$ of 0.751 (Table S3). The probability of identity (PID), that is, the probability for two individuals of having the same genotype, estimated with Cervus, was of 1.66×10^{-10} .

3.1 | Inferring parent-offspring relationships

Family relationships were inferred by long-term observations on each of the study groups, since their habituation. We first inferred the parent-offspring relationships from behavioral data. The silverback of each group was always assumed to be the father of all offspring of that group. Mothers were inferred either because they were observed giving birth, lactating, or for elder offspring; maternity was based on the combination of different affiliative behaviors (e.g., spatial proximity, feeding, and social tolerance) and physical traits (e.g., nose print). The first step of our analysis was to compare these relationships inferred from behavioral data to those inferred from genetic data. Among the 28 individuals that we analyzed (27 immatures together with a mature female, RC1-F4, who transferred from RC2 to RC1), we were able to genetically identify both parents for 20 offspring with Cervus (16 individuals at the 95% level and four individuals at the 80% level) and 15 offspring with RELPAIR (Table S4). Among the eight remaining cases, we separately assigned the mother for three individuals and the father for seven individuals with Cervus. Five of these seven individuals belonged to the RC2 group. Overall, among the 50 relationships where Cervus made a reliable inference (40 for RELPAIR; Table S4), only two discrepancies between the inferred relationships from field observations and the genetic data were identified and were similar for both Cervus and RELPAIR. These discrepancies corresponded to the paternity of two males in the groups CAR1-IN6 and RC2-IN2 (in both cases the eldest offspring of their group). In both cases, the solitary silverback LSB2 was identified to be more likely the father than the silverback of their respective groups. This was particularly significant for CAR1-IN6 (significance level of 95% with Cervus, and a likelihood ratio ten times higher for the solitary silverback being the father compared to the group silverback with RELPAIR; Table S4), even if the silverback is also compatible with the offspring. Conversely, for RC2-IN2, the paternity attribution to LSB2 was only significant at the 80% level. This inferred paternity is, therefore, more doubtful, the true father being possibly an unsampled male. In any case, this offspring was quite unlikely to have been sired by its group silverback, since they were not compatible at two loci. Finally, the adult female RC1-F4 was found to be the daughter of the RC2 group silverback (by Cervus) and an adult female (RC2-F1) of the same group (by Cervus and RELPAIR), as predicted from field observations of the natal transfer.

3.2 | Contrasting intra- versus intergroups relatedness among adults

We first used RELPAIR to test for significant genetic relationships between adults. We found a significant full sibling relationship between two females from the CAR1 group (likelihood ratio of 41.5) and a parent-offspring relationship between two females from the two neighboring groups in RC (likelihood ratio of 29.1).

We then measured the QG and LR relatedness estimators, as well as the Loiselle kinship estimator and found a strong correlation between the three metrics (Table S5 and Figure S1, Pearson's coefficient: r = 0.841–0.948, p < .0001 for all three comparisons; N = 231 adult pairs). Given their similarity, and the fact that previous studies have shown that the QG estimator had a smaller variance for higher-order relationships (Blouin, 2003; Csilléry et al., 2006), we decided to keep only the QG estimator for further analyses.

We then investigated whether pairs of females within groups were more related than pairs of females taken at random in the whole population (Figure 2). We found that for three groups, there was not a significant excess of relatedness: CAR1 (p = .377), CAR2 (p = .905), and RC1 (p = .504), while it was significant for RC2 (p =.0128). Accordingly, we found that a similar proportion of female pairs was significantly related within groups (2/20 = 10%) and among groups (7/71 = 9.9%; Table S5). Among the seven pairs significantly related among groups, four corresponded to females from neighboring groups (three from RC and one from CAR, i.e., 2–10 km apart) and three to females from distant groups (all being between CAR1 or CAR2 and RC1, i.e., at 57–61 km from one another).

Moreover, we did not find that females were more related to the silverbacks of their group than to other silverbacks (p = .169), the average QG relatedness value between females and the silverback of their group being of -0.0112. Similar proportions of male-female pairs were found to be significantly related within and among groups (1/14 = 7.1% and 9/98 = 9.2%, respectively; Table S5). Among the nine pairs significantly related but from different groups, seven belonged to distant groups (57-61 km apart); all seven of these pairs included one individual from CAR1 or CAR2 and one from RC1.

3.3 | Influence of geographical distance on genetic differences

With regard to the population differentiation indices, we found that the R_{ST} value (better suited for microsatellite markers) was significant among distant groups (i.e., between RC and CAR groups, including all adults, $R_{ST} = 0.0821$, p = .0089). R_{ST} was however not significant when only females were included in the analysis, likely because of power issues due to a reduced sample size. Interestingly, we found a significant correlation between the $R_{ST}/(1-R_{ST})$ coefficient and the logarithm of geographic distance, both when we considered all adults (regression slope b = 0.0682, p = .0399) or only the females (regression slope b = 0.0652, p = .042; Figure 3). However,



FIGURE 2 Histogram of the expected average relatedness values within each group obtained by 10,000 random permutations of individuals among groups. The red arrow indicates where the observed value lies. The *p*-value was computed as the percentage of permutations where the expected values were greater than or equal to the observed value. All computations were performed with the function grouprel of the R package related (see *Methods*), and the graphs were also displayed using this function



FIGURE 3 Pairwise values of the population differentiation index $R_{ST}/(1-R_{ST})$ plotted against the logarithm of the geographical distance using all adults (left) or only female adults (right)

we could not investigate this relationship in males, given the limited adult male sample size.

Further, when merging the two CAR groups and the two RC groups, respectively, we found that that RC females were more related than females taken at random in the whole population (p = .0201), while it was not the case for CAR females (p = .686). Conversely, pairs of males were not found to be more related within each country than pairs of males from different countries (p = .347 for CAR and p = .886 for RC). When looking in more details at the relatedness among the eight silverbacks, we found that two out of

the 28 pairs were significantly related: one between neighboring silverbacks (CAR2 and LSB2, at 10 km apart) and one between distant silverbacks (CAR1 and RC1, 57 km apart; Table S5).

3.4 | Adult female spatial and genetic proximity

For 21 pairs of females belonging to the same group, we obtained both genetic relatedness estimators and spatial proximity data from field observations. In 38% of adult female dyad scans (N = 520), adult females were greater than 10 m from each other, in 33% of scans between 6 and 10 m, and in 29% of scans between 0.5 and 5 m. They were never found at less than 0.5 m away from each other or in physical contact. Overall, the spatial proximity between dyads of adult females (average number of dyad scans <10 m corrected for the number of hours of focal dyad sampling) did not correlate with their QG genetic relatedness (Spearman correlation r = 0.144, p = .594, N = 21; Figure S2).

4 | DISCUSSION

4.1 | Insights on western gorilla socioecology from paternity analysis

The two methods used to genetically reconstruct the familial relationships (Cervus and RELPAIR) were largely consistent with each other, with more power using Cervus compared to RELPAIR. In the majority of cases (25/27 using Cervus and 20/22 using RELPAIR), paternity analysis identified the group silverback as the father of the group's immature offspring. Nevertheless, both methods showed that in two of the study groups (CAR1 and RC2), the eldest nonadult was likely not the son of the group silverback, as also found in two previous studies on unhabituated groups (Arandjelovic et al., 2014; Hagemann et al., 2018).

Further investigations are needed to better understand why exceptions to the exclusive paternity of the silverback occur in this one-male polygynous species and under which social contexts. This is possible via transfer of pregnant females (Manguette, Breuer et al., 2020), with nonadults joining groups after group disintegrations, or through extragroup paternity, in which case it might suggest that even if the silverback of the group is siring the majority of the offspring, other males could contribute occasionally to reproduction, similarly to that observed in multimale groups of mountain gorillas (Bradley et al., 2005). However, from the literature, group formation was largely made by solitary males acquiring a harem (Breuer et al., 2010) and no evidence exists for group takeovers from other silverbacks. Importantly, if extragroup paternity does occasionally occur in western gorillas, the absence of a paternal relationship between the group silverback and a given group female cannot be reliably used to identify adult females or exclude them as offspring, as done in previous studies on unhabituated groups of this species (Arandjelovic et al., 2014; Bradley et al., 2007; Douadi et al., 2007). We observed here extragroup paternity only for male offspring, but it cannot be excluded that it may occur for female offspring in other instances.

The genetic analysis also provided insights on group age. Most immatures for which Cervus could reliably identify the father but not the mother were in the same group, RC2, which suggests that their mothers may have already left the group, and females have been found to leave older or weaker males to join younger (fitter) males (Baudouin et al., 2019; Manguette, Robbins et al., 2020). Indeed, the RC2 group composition (with very few adult females and quite a few older offspring) was in agreement with that of previously described old groups (Parnell, 2002). This is also consistent with the silverback's physical appearance (e.g., deflated crest, Breuer, personal observation). Thus, using genetic analysis during the habituation of a new gorilla group might not only help in assessing if the same group is being followed over time (Bradley et al., 2008), but also in determining whether the target group is of a suitable age to undergo habituation, by assessing whether the mothers of the immatures are still present in the group.

The adult female RC1-F4 was found to be the daughter of the silverback and an adult female of the RC2 group, as predicted from field observations (i.e., she was observed transferring from RC1 to RC2). This result provides an additional case to the body of evidence that natal transfers are more likely to occur between neighboring groups. This could eventually lead to an excess of within-group female relatedness (as observed in Bradley et al., 2007), given that dispersal is not random but proportional to the geographic distance, and thus, the genetic distance in the case of females. Female dispersal allows avoiding inbreeding, which could lead to the apparition of deleterious traits. Moreover, it improves reproductive success by limiting intragroup feeding competition. Therefore, western gorilla females seem to show unconditionally a strategy of natal dispersal by departing from the group in which they were born (Baudouin et al., 2019; Manguette, Robbins et al., 2020; Stokes et al., 2003).

4.2 | Intra- versus intergroup relatedness among females: insights into dispersal strategy

Among all postdispersing females, we found only two pairs of female siblings among the four habituated groups. Even though we found one pair of full sisters within the CAR1 group, the other female pair with a high level of relatedness was found among neighboring groups in RC. Apart from these two cases, permutation analysis showed that adult females were generally not more related within groups than expected at random (Figure 2), except for the RC2 group, which consisted only of two related females. While we cannot exclude that this lack of significant excess in within-group relatedness may be linked to some extent with the limits of our datasets (49 individuals, 10 microsatellites), our result is nevertheless consistent with field observations. Indeed, while co-transfers of adult females have been observed (Manguette, Breuer et al., 2020), they are rare, as in western gorillas, the timing of female voluntary transfer depends on the age of the offspring and male coercive strategies (Breuer et al., 2016; Harcourt & Stewart, 2007b; Manguette et al., 2019; Stokes et al., 2003). Our result is however in contrast with some previous results found in western gorillas (Arandjelovic et al., 2014; Bradley et al., 2007), but in line with others (Douadi et al., 2007; Inoue et al. 2013). These contrasting results may have resulted from biases in sampling nonhabituated gorillas from nest sites, that is, errors in attributing females to immature versus mature classes based on analysis of their genetic relationship with the silverback, their dung size,

Our general lack of kin association among adult female western gorillas within the same group is more in keeping with the hypothesis that nonphilopatric females are not expected to cooperate (Harcourt & Stewart, 2007b; Robbins & Robbins, 2018; Sterck et al., 1997; Watts, 1994). Field observations also corroborate this, showing little or no affiliative behavior among adult females within the same western gorilla group (Stokes, 2004; Masi 2020). Our results show that adult females spend little time in close proximity to each other (29% of observations between 0.5–5 m and none <0.5 m) and that their spatial distance does not correlate with their genetic distance, unlike what was found in other species (Kapsalis & Berman, 1996).

Further, we found no evidence that female western gorillas avoid transferring to related silverbacks, as females did not appear to be more related to the silverbacks of their group than to other silverbacks, contrarily to findings on nonhabituated gorillas (Douadi et al., 2007) or on mountain gorillas (Vigilant et al., 2015).

4.3 | Comparing genetic and geographical distances

Among the seven significantly related female pairs belonging to different groups, three pairs corresponded to females from the neighboring RC groups, with individuals apparently transferring between the two groups. In particular, as pointed out above, we showed that a mature female from the RC1 group was born in the RC2 group. However, three of the remaining related female pairs were from distant areas (between CAR and RC, 57-61 km apart), suggesting that multiple transfers of one or more related females dispersing further afield also occur occasionally, since females do not range alone (Breuer et al., 2010; Parnell, 2002; Stokes et al., 2003). The infrequency of such long-distance female transfers is corroborated by the fact that relatedness was found to be significantly higher among females within RC than across countries (Figure 4). In contrast, we did not find such a result for males, indicating that males disperse further than females, as has been previously suggested (Douadi et al., 2007).

Our findings are also consistent with field observations on western gorillas. Females transfer from one group to a neighboring group during intergroup encounters which likely does not range far from their natal group (Manguette, Robbins et al., 2020; Stokes et al., 2003). Later, both voluntary (e.g., predispersal, in aging groups) and involuntary (e.g., as a consequence of silverback death or group disaggregation) secondary transfers allow them to disperse wider, increasing the likelihood that they will reside in a group with no or little kin (Manguette, Robbins et al., 2020; Stokes et al., 2003). In contrast, males often spend months to years as solitaries while they reach maturity and gain sufficient experience to attract and protect females to form their own breeding group (Breuer et al., 2009; Breuer et al. *in preparation*); some males may never succeed in acquiring females. Thus, males can disperse much further from their natal group than females, particularly during the male propedeutical solitary phase. This may also be true for those that never succeed in acquiring females or those that later lost their females. While this longer dispersal distance for males may not be consistent with the hypothesis of a "dispersed male network" (Bradley et al., 2004), this result is in line with a similar- and large-scale study based on Y-chromosomal microsatellite markers of unhabituated western gorillas that found a single undifferentiated male population (Douadi et al., 2007; Inoue et al., 2013).

In addition, using the population differentiation index R_{ST} , we found that CAR and RC gorillas were genetically distinct, and we found a signal of isolation by distance as indicated by the significant relation observed between pairwise R_{ST} and geographical distance, whether considering all adults or females only (Figure 3). This is consistent with the clinical pattern found in a larger scale study also using microsatellite genotypes (~37,000 km², Fünfstück et al., 2014). Our finding suggests thus again that, although males can disperse further than females, dispersal overall is limited in this species.

4.4 | Comparison with other species—where do the western gorillas fit?

Our study showed that Gorilla is a genus where extragroup paternity is limited compared to other polygynous species such as lions (Lyke et al., 2013), which indicates a rather strict control of male gorillas over their group females, for example, via coercive behavior (Breuer et al., 2016). Moreover, as shown for mountain gorillas (Roy et al., 2014), we found a positive relation between geographical distances and genetic differentiation (Figure 3). While we did not find a higher-than-expected level of relatedness among females within groups, we found some evidence that dispersal by females is limited in this species (Figure 4) and that long-distance dispersal is more likely in males, as in other polygynous species such as elephant seals (Fabiani et al., 2003) or lions (Curry et al., 2020; van Hooft et al., 2018). In fact, polygyny may favor male-biased dispersal, as competition for females will lead to greater male dispersal, such as is seen in shore birds (D'Urban Jackson et al., 2017). Similarly, in other social animals, dispersing males occasionally transfer their genes over longer distances (Fabiani et al., 2003; Mech & Boitani, 2003).

5 | CONCLUSION

Overall, comparing our findings with previous studies, all carried out on unhabituated groups, our study exemplifies how results can be affected by geographical scale and the incorrect categorization of individual samples. In our study on habituated groups, the vast majority



FIGURE 4 Histogram of the expected average relatedness values within each country obtained by 10,000 random permutations of individuals among countries, for females (upper) and for males (lower). The red arrow indicates where the observed value lies. The *p*-value was computed as the percentage of permutations where the expected values were greater than or equal to the observed value. All computations were performed with the function *grouprel* of the R package *related* (see methods), and the graphs were also displayed using this function

of genetically inferred parent-offspring relationships matched field observations. Likewise, inferred paternities and maternities from genetic data were largely consistent with those inferred from field observations of gorillas residing in habituated groups. Together, our results strongly suggest that relatedness levels within and between sexes do not seem to be factors influencing female dispersal patterns in this species, contrarily to what was previously suggested (Bradley et al., 2007). Male reproductive strategies are rather the driver of dispersal in western gorillas—age and male fitness is key and impacts both male and female reproductive strategies, confirming previous studies (Breuer et al., 2012; Caillaud et al., 2008)—females pursue a strategy of secondary transfer and only rarely are able to confuse paternity (this study and Manguette, Breuer et al., 2020). Some exceptions and counterstrategies do exist but appear to be rare.

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CONFLICT OF INTEREST

The authors declare to have no conflicts of interest.

AUTHOR CONTRIBUTION

Shelly Masi: Conceptualization (lead); Data curation (lead); Formal analysis (supporting); Funding acquisition (lead); Investigation (lead); Methodology (equal); Project administration (lead); Resources (lead); Supervision (equal); Validation (equal); Visualization (supporting); Writing-original draft (lead); Writing-review & editing (lead). Frederic Austerlitz: Conceptualization (supporting); Data curation (supporting); Formal analysis (lead); Investigation (equal); Methodology (equal); Software (lead); Validation (equal); Writingreview & editing (equal). Chloé Chabaud: Formal analysis (supporting); Investigation (supporting); Methodology (supporting); Software (supporting); Visualization (supporting); Writing-original draft (equal); Writing-review & editing (supporting). Sophie Lafosse: Data curation (equal); Formal analysis (supporting); Funding acquisition (supporting); Resources (supporting). Nina Marchi: Data curation (equal); Formal analysis (supporting); Resources (supporting); Writing-review & editing (supporting). Myriam Georges: Data curation (equal); Formal analysis (supporting); Resources (equal). Françoise Dessarps: Data curation (equal); Formal analysis (supporting); Resources (equal). Silvia Miglietta: Data curation (equal); Formal analysis (supporting); Resources (equal). Andrea Sotto-Mayor: Data curation (equal); Formal analysis (supporting); Resources (equal). Aurore San Galli: Data curation (equal); Resources (equal). Ellen Meulman: Data curation (equal); Resources (equal). Emmanuelle Pouydebat: Data curation (equal); Funding acquisition (lead); Resources (supporting); Writing-review & editing (supporting). Sabrina Krief: Data curation (equal); Funding acquisition (lead); Methodology (supporting); Resources (supporting); Writing-review & editing (supporting). Angelique Todd: Data curation (supporting); Methodology (supporting); Resources (supporting); Writing-review & editing (equal). Terence Fuh: Data curation (supporting); Methodology (supporting); Resources (supporting); Writing-review & editing (supporting). Thomas Breuer: Data curation (supporting); Investigation (supporting); Methodology (supporting); Resources (supporting); Visualization (supporting); Writing-review & editing (equal). Laure Segurel: Conceptualization (lead); Data curation (equal); Formal analysis (lead); Funding acquisition (equal); Investigation (lead); Methodology (lead); Project administration (equal); Resources (equal); Software (lead); Supervision (equal); Validation (lead); Visualization (lead); Writing-original draft (equal); Writing-review & editing (lead).

DATA AVAILABILITY STATEMENT

All genetic data are deposited in Dryad https://doi.org/10.5061/ dryad.t4b8gtj1s. All genetic analyses were performed with publicly available programs.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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7.3 LES STATIONS DE TERRAIN DE LONG TERME ET LA BASE DE DONNEES

Notre équipe appuie ses recherches sur des données longitudinales collectées sur les primates dans leurs habitats, en Afrique (Madagascar, RDC, RCA, Ouganda) et en Asie (Indonésie, Japon). À ce titre, les stations de terrain jouent un rôle-clé dans les travaux de notre équipe. Ces terrains de long-terme sont des outils indispensables et précieux permettant de conduire des recherches originales sur des thématiques diverses.



BASE DE DONNEES "GRANDS SINGES"

Ces stations de recherche permettent le recueil de données uniques. Un travail interdisciplinaire collaboratif a été mis en place pour valoriser ces données de terrain collectées sur trois espèces de grands singes (gorilles de l'Ouest, bonobos, chimpanzés) dans trois sites en Afrique, sous la forme d'une **base de données 'GRANDS SINGES'**. Cette base créée en 2013 va permettre de croiser les entrées santé/comportement/écologie/site/espèce. Elle a déjà mobilisé de nombreux moyens humains et financiers au sein de deux unités du Muséum : l'UMS BBEES et l'UMR 7206 Eco-anthropologie. Ce travail inclut des chercheurs de IPE mais également des IR : la coordination est réalisée par Flora Pennec et Eric Gimel participe en temps qu''Administrateur "bases de données" pour l'UMR.

Le projet visant à optimiser ce travail par la réalisation d'une **interface web** a pour objectif de faciliter la saisie, l'analyse et surtout la consultation des données.



Capture d'écran de l'interface BDD