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Is it for real? Structural differences between play and real fighting in adult chimpanzees (*Pan troglodytes*)

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Abstract

In primates, as well as in other mammals, play fighting (PF) is a complex form of playful activity that is structurally similar to real fighting (RF) and may also be used in a competitive way. Here, we verify the structural key differences that can distinguish PF from RF in adult chimpanzees (*Pan troglodytes*). We collected 962 h of video recording on 30 adult individuals belonging to four chimpanzee groups (*Mona Chimpanzee Sanctuary*, Spain; *La Vallée des Singes* and *ZooParc de Beauval*, France). We applied different indices—two of which were borrowed from the ecological measures of biodiversity—to test for structural differences between PF (345 sessions) and RF (461 sessions) in the levels of behavior repetition (*Repeatability of Same Behavior Index*, RSBI), distribution uniformity (*Pielou Index*, J), variability (*Shannon Index*, H′) and, symmetry (i.e., reciprocal exchange of offensive/defensive behaviors; *Asymmetry Index*, AI). Moreover, we compared the session duration between PF and RF. We found that duration and RSBI were higher in PF than RF while AI was higher in RF than PF. No difference was found between J and H′. Interestingly, both females and males maintained similar ranking positions (determined via Normalized David's scores) in RF and PF. Our study indicates that session duration, behavior repetition, and symmetry can be distinctive structural key features of PF whereas dominance role-reversal, behavior variability, and distribution uniformity were not. PF in adult chimpanzees may have elements of serious contexts (e.g., absence of role-reversal as in RF) which is in line with the view that play is a blended, multifunctional behavior deriving from the re-combination of different behavioral systems. Our findings highlight the need to investigate play structure and manifestation in a nuanced way to better understand the actual motivation that underlies what appears to be play.

KEYWORDS
play fighting, real fighting, reciprocity, repetition, role reversal

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Abbreviations: AI, Asymmetry Index; BEA, ZooParc de Beauval chimpanzee colony; BIL, Bilinga group of Mona Chimpanzee Sanctuary; D, defensive behavior; E, facial expression; H′, Shannon Index; J, Pielou Index; MONA, Mona Chimpanzee Sanctuary colonies; MUT, Mutamba group of Mona Chimpanzee Sanctuary; N, neutral behavior; NDS, Normalized David's score; O, offensive behavior; PF, play fighting; RF, real fighting; RSBI, Repeatability of Same Behavior Index; V, vocalization; VDS, La Vallée des Singes chimpanzee colony.

1 | INTRODUCTION

During play in primates and other animals, motor patterns from diverse behavioral domains can be recruited and combined in different ways (Fagen, 1981; Pellis & Burghardt, 2017). For this reason, it has been proposed that play may be a specific and independent behavioral system (Pellis & Burghardt, 2017; Pellis et al., 2019).

Based on the previous literature (Burghardt, 2005, 2011), a behavior should satisfy five criteria to be recognized as play: (i) not having (for the observer) an evident resource (e.g. food, sexual partner) to compete for, (ii) being voluntary and rewarding, (iii) including patterns that are incomplete, exaggerated and variable in their form and timing, (iv) being composed of repeated but not stereotyped or abnormal patterns, and (v) occurring in absence of serious environmental/physical stressors.

Human and nonhuman primates can engage in different types of play (e.g., object play, solitary play; Burghardt, 2005; Cordoni & Palagi, 2011; Pellegrini & Smith, 1998), and one of the most complex is play fighting (or Rough-&-Tumble; Smith, 1989). During play fighting primates can engage in interactions that—although not entirely—largely reflect the performance of agonistic behaviors during real fighting (Cordoni et al., 2022a; Palagi et al., 2016; Pellis & Pellis, 2017). Unless it escalates into aggression, play fighting is not usually associated with injuries and subjects do not protect an evident resource (Smith, 1997). Moreover, during play fighting primates can display specific facial expressions, body postures, or vocalizations to signal the “benign” intents of the subjects involved (Cordoni & Palagi, 2012; Iwaniuk et al., 2001; Kerney et al., 2017; Palagi et al., 2016; Pellis & Pellis, 1996; Pellis et al., 2015; Smith, 1989, 1997). Play fighting can be affected by individual (e.g., species, age, gender, and neural traits), social (e.g., affinitive and dominance relationships), and environmental (e.g., food abundance and predator presence) factors (Fagen, 1981; Pellis & Pellis, 2017). Even though play fighting is more frequent in immature individuals, in some primate species it is also retained and variably expressed in adulthood (e.g., *Propithecus verreauxi*—sifakas, Antonacci et al., 2010; *Pan paniscus*—bonobos, Palagi & Cordoni, 2012; Palagi, 2006; *Pan troglodytes*—chimpanzees, Yamanashi et al., 2018; *Gorilla gorilla gorilla*—lowland gorillas, Cordoni et al., 2022b). For example, in bonobos play fighting is maintained at relatively high levels between adults (Palagi & Cordoni, 2012). As in juvenile individuals, in adult primates play fighting may serve both long-term benefits—such as social assessment and social status determination—and short-term benefits—such as conflict prevention (Antonacci et al., 2010; Norscia & Palagi, 2011; Palagi & Cordoni, 2012; Paquette, 1994).

Play has been considered as a potential animal welfare indicator (Oliveira et al., 2010) because (i) it often disappears when individuals are under serious stressful conditions/states and fitness challenge (Burghardt, 2005; Fagen, 1981) and (ii) it is thought to be accompanied by a pleasurable emotional and rewarding experience (Panksepp, 2022; Pellis & Pellis, 2009; van Kerkhof et al., 2013; Vanderschuren et al., 2016; Vanderschuren, 2010). However, some studies revealed that—depending on the species—play fighting in adults can contribute in the short-term to buffer transient anxiety or be positively correlated with the levels of chronic stress and/or aggressive interactions (chimpanzees: Palagi et al., 2004; Yamanashi et al., 2018; bonobos: Palagi et al., 2006; monkeys: Norscia & Palagi, 2011; lemurs: Norscia & Palagi, 2016). Yamanashi et al. (2018) demonstrated that among adult chimpanzees play fighting levels correlated with aggression but not with grooming levels and that play fighting can be used for tension reduction. Hence, play is not always an indicator of individual positive emotional state. Under specific conditions, play fighting may be promoted by an adverse psychological or emotional state and may increase individual emotional resilience (Held & Špinka, 2011; Špinka et al., 2001) and the ability to cope with stressful and agonistic contests (Hausberger et al., 2012; Oliveira et al., 2010).

As in many mammals, primates perform many behaviors during “non-serious fighting” (i.e., play fighting; Bekoff & Allen, 1998; Bekoff, 2014) that are reflective of behaviors performed during “serious fighting” (i.e., aggression or real fighting). Play fighting may provide practice of tactics that can be similar to those used in real fighting even though play fighting does not completely mirror real fighting, especially in the way behavioral patterns are performed (Briffa & Lane, 2017; Burghardt, 2005; Symons, 1978). Hence, play fighting may represent an alternative way to acquire and test skills and knowledge when there are risks of doing so through direct experience (e.g., real fighting; Bock & Johnson, 2004). For example, in sifaka (*Propithecus verreauxi*) adult males can play with out-group members to overcome xenophobia and avoid conflict with non-familiar individuals (ice-breaker effect, short-term benefit; Antonacci et al., 2010). In howler monkeys (*Alouatta palliata*), play between adults may act as a tool to regulate competition and promote social tolerance (short-term benefit; Asensio et al., 2022). Through play fighting juvenile lowland gorillas (*Gorilla gorilla gorilla*) can manage the competition before the distribution of food thus avoiding direct confrontation (short-term benefit; Palagi et al., 2007). In chimpanzees (*Pan troglodytes*) play fighting acquires more competitive elements during juvenility thus permitting an efficient self- and social-assessment process (long-term benefit; Cordoni & Palagi, 2011; Palagi & Cordoni, 2012; Paquette, 1994). In humans, several hunter-gatherer groups often performed coalitional play fighting that in the long term can improve skills involved in coalitional real fighting (Sugiyama et al., 2018).

The current study aims at evaluating in a quantitative and replicable way how fighting in the play context structurally differs from fighting in the aggressive context. To achieve this goal, we gathered behavioral data on chimpanzees because they (i) show adult-adult play fighting both in captive and wild conditions (Matsusaka, 2004; Palagi & Cordoni, 2012; Palagi, 2006; Yamanashi et al., 2018) and (ii) are the species phylogenetically closest to humans (along with bonobos; Langergraber et al., 2012). Hence, studying chimpanzee behavior allows inferences about the evolutionary processes at the basis of the connection between play and real fighting in humans.

Chimpanzees live in a fission-fusion society and adult males—particularly maternal brothers—form strong and long-lasting affiliative and cooperative bonds (Bray & Gilby, 2020; Gilby & Wrangham, 2008; Langergraber et al., 2007; Mitani, 2009). Females are the dispersing sex (Pusey, 1980) and may not form tight social relationships, even though this situation can vary across different populations and ecological conditions (Emery Thompson et al., 2007; Wakefield, 2008, 2013; Watts, 2012).

To quantify the possible structural key features that can allow the distinction between play fighting and real fighting in adult chimpanzees, we tested the following predictions.

1.1 | Prediction 1

Animals can interrupt and resume play in an atypical rhythm by generating different chains of actions with various mixed-up behavioral patterns (Pisula, 2008). Previous literature shows that play fighting—compared with real fighting—can show increased behavior repetition, variability, and distribution (Burghardt, 2005; 2011; Cordoni et al., 2022a). Hence, we expected that in adult chimpanzees the general levels of behavioral pattern repetition (e.g. how many times the same behavior follows itself within a session), variability (e.g. how many types of behavioral patterns are performed in a session), and distribution uniformity (i.e., how many times the same type of behavioral pattern is performed within a session in relation to other pattern distribution) within sessions would be higher in play fighting rather than in real fighting (*Prediction 1a*).

Play is considered a pleasurable activity and may be rewarding for players (Burghardt, 2005, 2011; Pellis & Pellis, 2009; Trezza et al., 2010; van Kerkhof et al., 2013; Vanderschuren et al., 2016; Vanderschuren, 2010). As such players should be motivated to continue playing. Indeed, at the neural level the facilitation of the expression of play can increase the duration of playful session (e.g., van Kerkhof et al., 2013). On the other hand, aggression is not at all pleasurable and—as a social stressor—can cause an increase in cortisol levels with deleterious physical effects on subjects (Muller et al., 2021; Schrock et al., 2019). Individuals should therefore be motivated to reduce its duration as much as possible. Hence, even though either play fighting or real-fighting sessions can markedly vary in session length, we expected that the duration of the session would be higher in play fighting rather than in real fighting (*Prediction 1b*).

1.2 | Prediction 2

In primates, competition during play fighting can be balanced—at least up to a certain extent—by cooperation (e.g., via self-handicapping, role-reversal, and reciprocity; Bauer & Smuts, 2007; Pellis & Pellis, 2017; Pellis et al., 2010; Petrů et al., 2009). This balancing mechanism is necessary to sustain play and reduce the probability of escalation into serious aggression (Bekoff, 2014; Pellis & Pellis, 1988; Reinhart et al., 2010). During real fighting competition is not balanced by cooperation: individuals compete fiercely to gain an advantage over their competitors so as to acquire dominant positions and/or obtain priority access to resources (de Boer and Koolhaas (2017); de Koolhaas et al., 2013; Norscia & Palagi, 2016). Thus, we expected that in adult chimpanzees the levels of behavioral symmetry (i.e. in terms of reciprocity in offensive and defensive behavioral patterns) between interacting subjects would be higher in play fighting than in real fighting (*Prediction 2a*). If so, we also expected that individual dominance positions (deriving from the use of offensive vs defensive behaviors) in play fighting would not correlate with individual dominance positions in real fighting (*Prediction 2b*).

2 | METHODS

2.1 | The study groups

The present study was carried out on four groups of chimpanzees (*Pan troglodytes*; see Table 1) that are described in details below.

Mona Chimpanzee Sanctuary. Two of the study colonies were housed at the Mona Chimpanzee Sanctuary, a rehabilitation center managed by Fundaciòn MONA (Riudellots de la Selva, Spain). Each group—named Bilinga (BIL; $N_{\text{females}} = 3$, $N_{\text{males}} = 4$, age range = 18–37 years, mean age of adults = 29.9 ± 6.5 SD) and Mutamba (MUT; $N_{\text{females}} = 2$, $N_{\text{males}} = 5$, age range = 16–36 years, mean age of adults = 25.4 ± 8.1 SD), respectively—was composed of seven unrelated individuals. The females of both groups were treated with oral contraceptives and only one male (Victor) belonging to BIL group had been castrated before its arrival at the sanctuary. Both groups occupied similar indoor (50 m^2 BIL; 45 m^2 MUT) and outdoor (3220 m^2 BIL; 2420 m^2 MUT) facilities. Chimpanzees received food (i.e., fruits, vegetables, juice, dried fruits, seeds, and rice) scattered on the ground five times per day.

La Vallèe des Singes (Romagne, France). The group was composed of six unrelated chimpanzees ($N_{\text{females}} = 3$, $N_{\text{males}} = 3$, age range = 12–26 years, mean age of adults = 20.8 ± 6.5 SD). In October 2019 a new female—Lila—joined the group. Females were not treated with oral contraceptives and males were not castrated. The animals could freely move back and forth an indoor of about 200 m^2 and an island of about 3000 m^2 surrounded by a moat. Chimpanzees received food (i.e., vegetables, fruit, seeds, and pellets) scattered on the ground four times per day.

ZooParc de Beauval (Saint Aignan sur Cher, France). The group was composed of 16 individuals ($N_{\text{adult\_females}} = 8$, $N_{\text{adult\_males}} = 2$, age range = 15–46 years, mean age of adults = 35.6 ± 9.2 SD). Six females of the group (Baraka, Bonobo, Charlotte, Julie, Sangha, and Wamba) were treated with oral contraceptives and three males (Lukombé, Gamin, and Tumba) have got vasectomy. Chimpanzees occupied an indoor facility of about 300 m^2 and an island surrounded by a moat of 3000 m^2. The animal received food (i.e., vegetables, seed/pellet cake, and fruits) scattered on the ground seven times per day.

The equipment of indoor and outdoor facilities of the four colonies was similar and included platforms, ropes, trunks,

TABLE 1 The four chimpanzee colonies observed in this study.

Subject	Gender	Age* (years)	Colony
Juan	m	16	MONA (MUT)
Nico	m	18	MONA (BIL)
Bongo	m	19	MONA (MUT)
Africa	f	20	MONA (MUT)
Waty	f	22	MONA (MUT)
Coco	f	25	MONA (BIL)
Cheeta	f	29	MONA (BIL)
Charlie	m	30	MONA (MUT)
Tico	m	32	MONA (BIL)
Bea	f	34	MONA (BIL)
Tom	m	34	MONA (BIL)
Marco	m	35	MONA (MUT)
Toni	m	36	MONA (MUT)
Victor	m	37	MONA (BIL)
Lila	f	12	VDS
Cauna	f	13	VDS
Wonder	m	24	VDS
Roy	m	25	VDS
Conan	m	25	VDS
Kika	f	26	VDS
Sangha**	f	15	BEA
Micheline	f	31	BEA
Gamin**	m	32	BEA
Domi	f	32	BEA
Gypso	f	34	BEA
Bonobo	f	39	BEA
Julie	f	39	BEA
Baraka**	f	42	BEA
Joseph**	m	46	BEA
Charlotte	f	46	BEA

Abbreviations: BEA, ZooParc de Beauval; MONA, Mona Chimpanzee Sanctuary; VDS, La Vallée des Singes.

*At the time of the observations.

**Individuals belonging to the Beauval colony that were included in the analyses.

hammocks, straw, and vegetation. Environmental enrichments such as artificial termite nest and task maze were also provided. All the chimpanzees belonging to the four colonies were in continuous full contact (i.e., housed together and in complete tactile contact).

In our analyses we included only individuals that were sexually mature (Walker et al., 2018) and that showed both play and real fighting interactions ($N = 24$ adult individuals; Table 1). No difference was found in the age (in years) distribution of the individuals across groups (Kruskal–Wallis test $N = 24$, $\chi^2 = 5.034$, $df = 3$, $p = 0.169$; mean age value ± SD: 28.93 ± 9.37; age range: 12–46).

Hereafter, we labeled the four colonies as follow: MONA (*Mona Chimpanzee Sanctuary*; both MUT and BIL group), VDS (*La Vallée des Singes*), and BEA (*ZooParc de Beauval*).

2.2 | Data collection

Video-data on the four colonies were collected by five observers (G.Co., G.Ci, A.Pa., V.B., and I.N.) during the following periods: February–July 2019 MONA, April–December 2019 and August–September 2020 VDS, May–October 2021 BEA. Videos were recorded via Full HD, Panasonic HDC-SD9 e HC-V380/V180 cameras (optical zoom 50x, frame rate: 60fps; precision 2csec). Before the start of systematic video collection, all the observers were trained for 40 h by G.Co. in animal distinction, behavioral pattern identification (see Table 2) and video-recording procedures. Training finished when the interobserver reliability score—measured via Cohen's k—ranged from 0.80 to 0.90. The videos were then analyzed, frame-by-frame and or in slow-motion, by using the software freeware Avidemux 2.7.1. We collected a total of 962 h of video-recording.

Via the all occurrences sampling method (Altmann, 1974) we gathered all adult-adult play and real fighting sessions. In particular, for each event we recorded: (i) identity of the subjects involved and their features (i.e., sex, age, and group), (ii) behavioral patterns performed and their exact chronological order (see Table 2), and (iii) duration (in seconds) of the interaction. By this method we recorded a total of 345 play fighting and 461 real fighting sessions among adult chimpanzees. We never observed adult–adult play fighting escalating into real fighting and/or behaviors exclusive of play fighting occurring during real fighting.

2.3 | Operational definitions

A real fighting started when a chimpanzee directed a behavioral pattern exclusive to the aggressive domain (Table 2) towards a companion and it ended with one of the opponents moving or running away. A play fight started when a chimpanzee directed a behavioral pattern exclusive of the play domain (Table 2) towards a group mate and finished when both players stopped the interaction, one of them moved away or a third individual substituted one of the two players or interrupted the session by dividing the two players (Palagi, 2008). We never observed any polyadic (i.e., more than two players) sessions between adults; hence, our analyses focused on dyadic play fights.

For both play fighting and real fighting, two consecutive sessions were considered as different if the interaction stopped for more than 10 s. For both contexts, we defined *decided* for those interactions during which it was possible to clearly distinguish between *winners*

TABLE 2 Behavioral patterns considered in this study for play fighting and real fighting in adult chimpanzees (see the text for definition of N, O and D categories).

Patterns exclusive of play fighting	
Full play face^{E}	The chimpanzee opens her/his mouth with both upper and lower teeth exposed (Preuschoft & van Hooff, 1995)
Laugh^{V}	Pant-like vocalization involves a series of low-frequency staccato grunts (Davila-Ross & Palagi, 2022; Gervais & Wilson, 2005)
Peek a boo^{N}	The chimpanzee hides and suddenly pops out from a shelter
Play eye cover^{O}	The chimpanzee covers with her/his hands the eyes of the playmate by making difficult playmate orientation in the environment
Play face^{E}	The chimpanzee opens her/his mouth with only the lower teeth exposed (Preuschoft & van Hooff, 1995)
Somersault^{N}	The chimpanzee flips over the ground or on vertical support in solitary or social manner
Patterns exclusive of real fighting	
Avoid^{D}	The chimpanzee moves away from the path when another individual is approaching her/him or takes a less direct route around the other
Bared-teeth^{E}	The chimpanzee's mouth corners are withdrawn and the lips retracted from teeth and gums. The mouth can be kept closed or slightly opened. It can be associated with screaming (Waller & Dunbar, 2005)
Bob^{D}	The chimpanzees bends her/his back and weaves with head or whole body in a bowing position upwards or forward (Roberts et al., 2014). This is a typical submissive behaviors that can be performed by subordinates to avoid being attacked
Charging display^{O}	The chimpanzee performs specific postures, movements, piloerection, facial expressions and vocalizations for threatening the opponent
Crouch/Crawl^{D}	The chimpanzee bends all four limbs, presses her/his *ventrum* to the ground, and tries to travel while in this position or crouches while sitting by lowering the head, hunching the shoulders, and often covering the head with her/his arm/s
Pant-grunt^{V}	Pant-grunt is an acoustically heterogeneous signal usually consisting of repeated grunts that can be panted and graded into barks or screams (Laporte & Zuberbühler, 2010)
Scream^{V}	The chimpanzee emits a high-pitched, high-volume frightened vocalization
Patterns shared by play and real fighting	
Bite^{O}	The chimpanzee closes her/his mouth on the partner's body
Flee^{D}	The chimpanzee runs away from the partner that runs behind her/him. While running away the chimpanzee often changes her/his direction, sometimes stops and looks back to check for the presence of the partner
Hide^{D}	The chimpanzee moves behind another subject or a part of the environment to place herself/himself out of other individual' sight
Jump^{O}	The chimpanzee jumps on the other subject only with feet generally in a quite bipedal position
Kick^{O}	The chimpanzee uses her/his feet to hit the other subject
Pull^{O}	The chimpanzee moves the other subject towards her/him with hands and feet
Push$^{O/D}$	The chimpanzee displaces the other subject far from her/him with hands/feet. The chimpanzee can perform a push for defending herself/himself from the attack of another subject or for attacking another subject
Retrieve^{O}	The chimpanzee blocks with her/his hands the other subject to prevent her/his moving away. It is different from pull that is generally performed with both feet and hands
Run after^{O}	The chimpanzee moves rapidly in quadrupedal position behind the other subjects that often changes her/his direction
Shake the rope^{O}	The chimpanzee strongly moves the rope on which the other subject is hanging
Shelter^{D}	The chimpanzee protects herself/himself from the attack of the other subject by putting her/his arms over the head
Slap^{O}	The chimpanzee hits with the palm of her/his open hand any part of the other subject's body
Stamp^{O}	The chimpanzee hits on the ground or on the other subject with her/his feet in a repeated way
Wriggle^{D}	The chimpanzee moves for getting rid of the grip of the other subject

Abbreviations: D, defensive behavior; E, facial expression; N, neutral behavior; O, offensive behavior; V, vocalization.

and *losers*. For real fighting, this could be determined when one individual (the loser) ran away and/or showed submissive/fear behaviors typical of the aggressive domain (Table 2) towards the opponent (the winner). For play fighting the winner was the individual that performed more offensive and/or less defensive behaviors than the other play mate (loser) (Bauer & Smuts, 2007; Cordoni et al., 2018; Ward et al., 2008). The behavioral patterns were classified as *Offensive* (O, unidirectional behaviors performed to attack the opponent), *Defensive* (D, behaviors aimed at eluding the attack by another individual), and *Neutral* (N, neither offensive nor defensive; Table 2).

In the analyses, we included sessions composed of at least two behavioral patterns to give both the interacting subjects the possibility to perform at least one behavior each.

Play and real fighting indices. For each play fighting and real fighting session, we calculated different indices to evaluate the distribution uniformity, repetition, and variability of the behavioral patterns performed within the session and the symmetry of the interaction.

2.3.1 | Repeatability of Same Behavior Index (RSBI)

The RSBI was calculated to evaluate the level of repetition of the same behavior within a single play/real fighting session (RSBI is an implementation of the Repetition Index by Collarini et al., 2022; Cordoni et al., 2022a). The index provides the measure of how many times the same behavior follows itself within a session. RSBI is a modified version of the Number of Transition Index suggested by Pelletier et al. (2020) for measuring human life course complexity as a function of number of state transitions. RSBI was calculated by counting how many times the same behavior followed itself within a session and dividing this value by the total behaviors composing session -1 (see below).

$$\text{RSBI} = \frac{(\text{times a same behavior follows itself})}{(\text{total patterns composing the session} - 1)}$$

For example, in a play session where a behavior “A” is repeated seven times, resulting in the pattern “AAAAAAA,” the RSBI is equal to six repetitions out of six total patterns (i.e. 7-1) resulting in 1.0 index value. Again, in a session composed of “AABBCCDDEE” there are five repetitions out of nine total patterns (i.e. 10-1) resulting in an index of 0.56. The index ranges from 0 to 1 for all session duration.

2.3.2 | Asymmetry Index (AI)

This index was used to quantify the level of play/real fighting symmetry in terms of reciprocity in offensive and defensive behaviors exchanged between subjects (Cordoni et al., 2016, 2018). It was calculated as follows: “the number of offensive behaviors by A towards B *plus* the number of defensive behaviors by B towards A” subtracted from “the number of offensive behaviors by B towards A *plus* the number of defensive behaviors by A towards B” divided by “the total number of behaviors performed by both individuals”. The formula of AI is reported below:

$$\text{AI} = \frac{(\text{offensive}_{A\to B} + \text{defensive}_{B\to A}) - (\text{offensive}_{B\to A} + \text{defensive}_{A\to B})}{(\text{total number of behaviors performed by both } A \text{ and } B)}.$$

AI ranges from −1 to +1 with main values indicating (i) a complete symmetry of the session (zero), (ii) a complete asymmetry of the session in favor of A (+1), and (iii) a complete asymmetry of the session in favor of B (−1).

2.3.3 | Diversity indices

We employed two indices used for measuring biodiversity in ecological studies (Lakićević & Srđević, 2018; Morris et al., 2014; Türkmen & Kazanci, 2010) and we adapted them to play fighting and real fighting. *Shannon index* (H′; also known as Shannon's diversity index, Shannon–Wiener index, Shannon–Weaver index, and Shannon entropy) is the most common diversity index used in ecological studies and it focuses on species richness (Keylock, 2005; Shannon, 1948). The mathematical formula of *Shannon index* is:

$$H' = -\Sigma[(n_i/N)*(ln\ n_i/N)].$$

In particular, n_i is the number of individuals belonging to the species i and N is the total number of individuals in a specific ecosystem. H′ values are generally between zero and five; when they are equal or higher than four indicate a great level of biodiversity. In our study n_i is represented by numbers of behaviors belonging to the type i and N are represented by the total number of behaviors composing a session. For example, a session of the following composition “AAABBC” has these n_i/N values 3/6 (AAA), 2/6 (BB), and 1/6 (C) and an H′ value of 1.011. Again, a session composed of “AABCDE” has an H′ value of 1.56. A high value of H′ indicates a great behavioral pattern variability in terms of different types of behaviors performed in a single session.

Pielou index (J; also known as Species evenness) derives from *Shannon index* and is the measure of the distribution of individuals among species within a specific ecosystem (Pielou, 1966). The mathematical formula of *Pielou index* is:

$$J = H'/H'_{\max}$$

H′ is the observed value of *Shannon index*, $H'_{\max}$ is the ln$S$ with S representing the total number of species. The values of J vary between zero and one: when they are close to one it means that individuals are evenly distributed among species (Pielou, 1966). In the present study, J was used to evaluate the level of uniformity in the distribution of behaviors within a session. Regarding the formula, S is represented by the number of different types of behavioral patterns. For example, a session of the following composition “AABC” has a S

value equal to 3 and a J value of 0.75. Again, a session composed of "ABCD" has a J value of 1.0. A high value of J indicates a uniform distribution of behaviors among the different types of playful/aggressive behavioral patterns.

Finally, we calculated the dyadic mean values of both play fighting and real fighting session duration in seconds. Moreover, we determined the session length also by calculating at the dyadic level the mean number of behaviors composing play/real fighting sessions.

2.4 | Statistical analyses

We compared play fighting and real fighting indices (*Prediction 1a* and *2a*) and durations (*Prediction 1b*) by carrying out paired analyses involving the same dyads in the two contexts. We tested the normality of data distributions by applying the Shapiro–Wilk test ($0.562 \le W \le 0.975$, $0.001 \le p \le 0.759$; Siegel & Castellan, 1988). For normal distributions (Shapiro–Wilk test $p \ge 0.05$), we applied the randomization paired *t*-test for two dependent samples by using the freeware Resampling Procedures (1.3 David C. Howell); 10.000 permutations were applied owing to data pseudo-replication caused by the same individuals being included in different dyads. For non-normal distributions (Shapiro–Wilk test $p < 0.05$), we applied the Wilcoxon test for two dependent samples with Monte Carlo randomization (10.000 permutations) owing to data pseudo-replication.

For each adult chimpanzee, we calculated the individual Normalized David's Score (NDS) on the basis of the observed outcomes of dyadic play/real fighting sessions (number of interactions won or lost by each subject; de Vries et al., 2006; de Vries, 1993). We calculated two different sets of NDS for each chimpanzee, one by using *decided* real fighting sessions ($\mathrm{NDS}_{\mathrm{real\_fighting}}$) and one by using *decided* play fighting sessions ($\mathrm{NDS}_{\mathrm{play\_fighting}}$; see *Operational definition*). In the measure of NDS the observed proportion of wins was corrected for the chance occurrence of the observed outcome based on binomial distribution with each subject having an equal chance to win or lose in every play/real fighting. The correction is necessary when, as in the case of our study, the number of play/real fighting greatly differed between pairs. Then we checked for a possible correlation between individuals $\mathrm{NDS}_{\mathrm{real\_fighting}}$ and $\mathrm{NDS}_{\mathrm{play\_fighting}}$ values and carried out separated analyses for females and males. We employed Spearman correlation test for nonnormal distribution and the Pearson correlation test for normal distribution (Siegel & Castellan, 1988; *Prediction 2b*). The nonparametric analyses were performed by SPSS 28.0. The significant threshold was set to $\alpha = 0.05$.

3 | RESULTS

3.1 | Prediction 1

We found that values of *Repeatability of Same Behavior Index* (RSBI) were higher for play fighting than for real fighting sessions ($\mathrm{RSBI}_{\mathrm{play\_fighting}} > \mathrm{RSBI}_{\mathrm{real\_fighting}}$; Wilcoxon test $N_{\mathrm{dyads}} = 26$, $T = 34$, ties = 3, $p < 0.001$; mean value ± SE: $\mathrm{RSBI}_{\mathrm{play\_fighting}}$ 0.246 ± 0.034, $\mathrm{RSBI}_{\mathrm{real\_fighting}}$ 0.113 ± 0.042; Figure 1).

No difference between play fighting and real fighting sessions was found for both Shannon (H′) and Pielou (J) indices ($H'_{\mathrm{play\_fighting}} \ne H'_{\mathrm{real\_fighting}}$; Randomization Paired *t*-test $N_{\mathrm{dyads}} = 26$, $t = -1.014$, $df = 25$, $p = 0.308$; mean value ± SE: $H'_{\mathrm{play\_fighting}}$ 1.250 ± 0.130, $H'_{\mathrm{real\_fighting}}$ 1.105 ± 0.086; $J_{\mathrm{play\_fighting}} \ne J_{\mathrm{real\_fighting}}$; randomization paired *t*-test $N_{\mathrm{dyads}} = 26$, $t = 0.428$, $df = 25$, $p = 0.662$; mean value ± SE: $J_{\mathrm{play\_fighting}}$ 0.716 ± 0.054, $J_{\mathrm{real\_fighting}}$ 0.746 ± 0.064). In sum, the same behavioral pattern followed itself significantly more frequent within a play fighting than a real fighting session but no difference was found in behavioral pattern variability and distribution uniformity in the two types of interactions.

We found that the mean duration (seconds) of play fighting sessions was significantly higher than the mean duration of real fighting sessions ($\mathrm{Duration}_{\mathrm{play\_fighting}} > \mathrm{Duration}_{\mathrm{real\_fighting}}$; randomization paired *t*-test $N_{\mathrm{dyads}} = 26$, $t = -4.535$, $df = 25$, $p < 0.001$; mean value ± SE: $\mathrm{Duration}_{\mathrm{play\_fighting}}$ 87.50 ± 13.80, $\mathrm{Duration}_{\mathrm{real\_fighting}}$ 20.02 ± 2.76; Figure 2). The mean values of session behaviors were higher for play fighting than for real fighting (Wilcoxon test $N_{\mathrm{dyads}} = 20$, $T = 3.0$, ties = 0, $p < 0.001$; mean value ± SE: play fighting 19.00 ± 3.00, real fighting 5.60 ± 0.823).

3.2 | Prediction 2

By comparing the sessions performed by the same dyads, we found that the Asymmetry Index values were higher for real fighting than for play fighting ($\mathrm{AI}_{\mathrm{real\_fighting}} > \mathrm{AI}_{\mathrm{play\_fighting}}$; randomization paired *t*-test $N_{\mathrm{dyads}} = 26$, $t = 2.777$, $df = 25$, $p = 0.0085$; mean value ± SE: $\mathrm{AI}_{\mathrm{real\_fighting}}$ 0.410 ± 0.061, $\mathrm{AI}_{\mathrm{play\_fighting}}$ 0.165 ± 0.075; Figure 3).

For both females and males $\mathrm{NDS}_{\mathrm{real\_fighting}}$ positively correlated with $\mathrm{NDS}_{\mathrm{play\_fighting}}$ (Spearman correlation test $N_{\mathrm{females}} = 15$, $r_S = 0.818$, $p < 0.001$; Pearson correlation test $N_{\mathrm{males}} = 15$, $r = 0.715$, $p = 0.003$; Figure 4). Thus, female and male chimpanzees possessing dominant positions in real fighting maintained such positions in play fighting as well.

4 | DISCUSSION

In the current study, we showed that in adult chimpanzees play fighting and real fighting can be structurally distinguished even though not always as expected following the indications of previous literature (Burghardt, 2005, 2011; Cordoni et al., 2022a; Smith, 1997). Behavioral patterns were more frequently repeated during play fighting than real fighting sessions, but their level of variability and distribution uniformity did not differ between the two types of interaction (*Prediction 1a* partially supported; Figure 1). Compared with real fighting sessions, play fighting sessions were longer (*Prediction 1b* supported; Figure 2) and included more of a symmetrical exchange of offensive and defensive behaviors

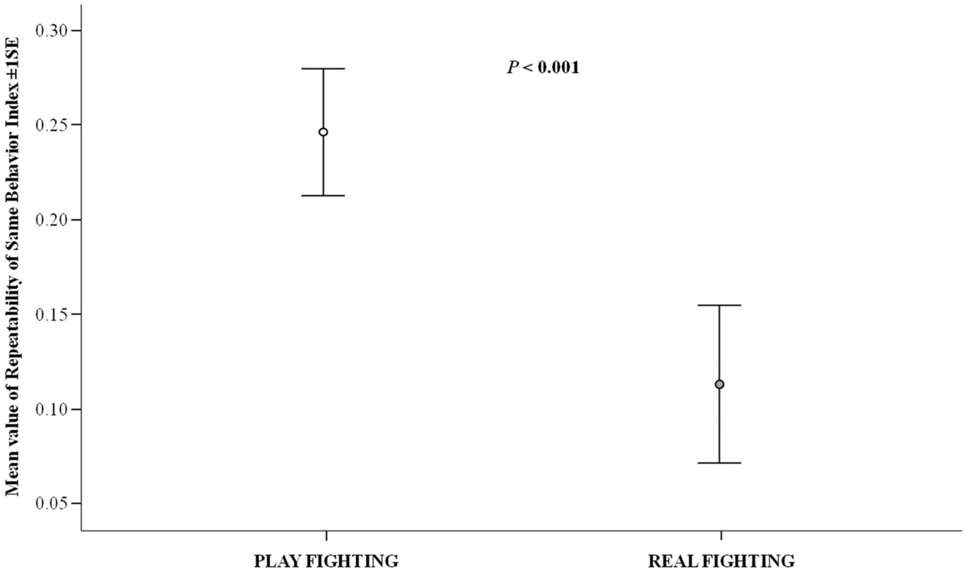

FIGURE 1 Error bars showing on Y-axis mean values (±1SE) of the Repeatability of Same Behavior Index (RSBI) as a function of play fighting and real fighting (X-axis).

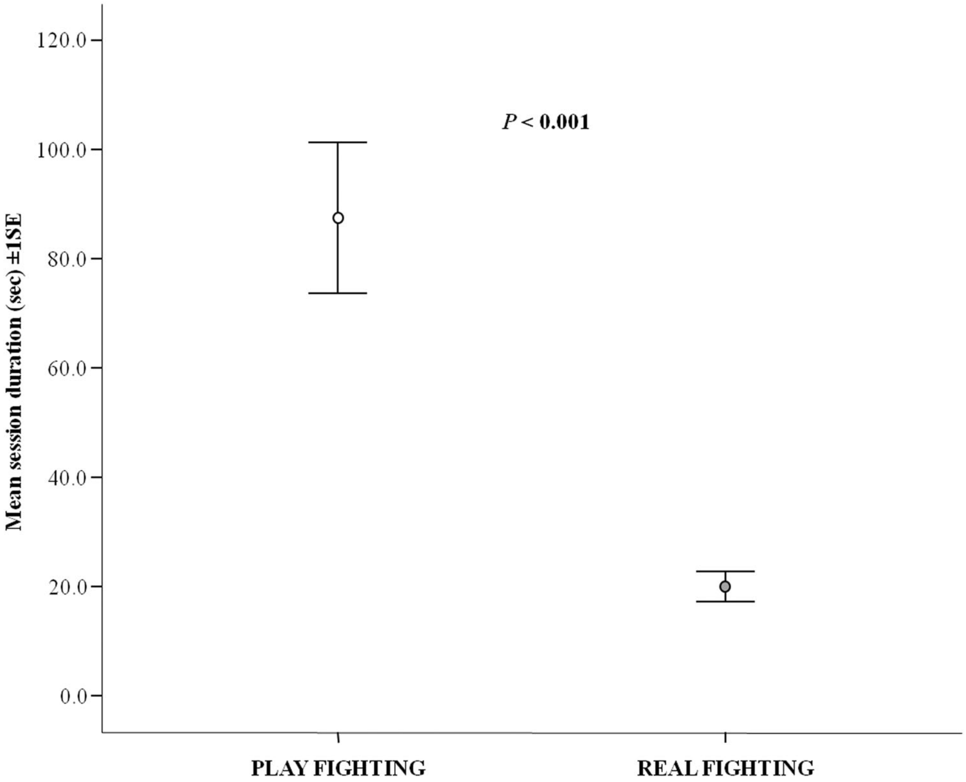

FIGURE 2 Error bars showing on Y-axis mean session duration (±1SE) in seconds as a function of play fighting and real fighting (X-axis).

(*Prediction 2a* supported; Figure 3). Despite this, male and female chimpanzees maintained the same dominance positions in both contests (*Prediction 2b* not supported; Figure 4).

In our study, we found that during play fighting adult chimpanzees repeated the same behavioral patterns than in real fighting (RSBI, Figure 1). Because behavioral pattern repetition - but not variability and distribution uniformity—was higher in play fighting than in real fighting sessions, we suggest that repetition can be confirmed as a key feature of play (*sensu* Burghardt, 2011) in adult chimpanzees. Indeed, repetition is a common characteristic of human and non-human play (Barbado Murillo et al., 2017; Burghardt, 2005; Jones et al., 2019). Although no specific studies are available in this

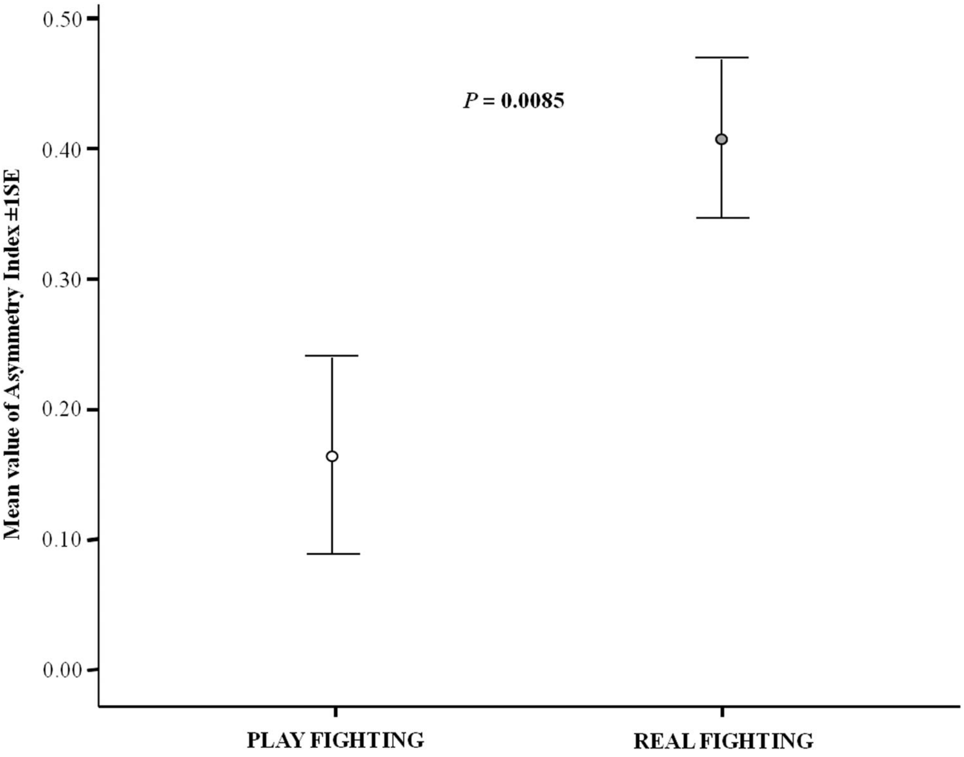

FIGURE 3 Error bars showing on Y-axis mean values (±1SE) of Asymmetry Index as a function of play fighting and real fighting (X-axis).

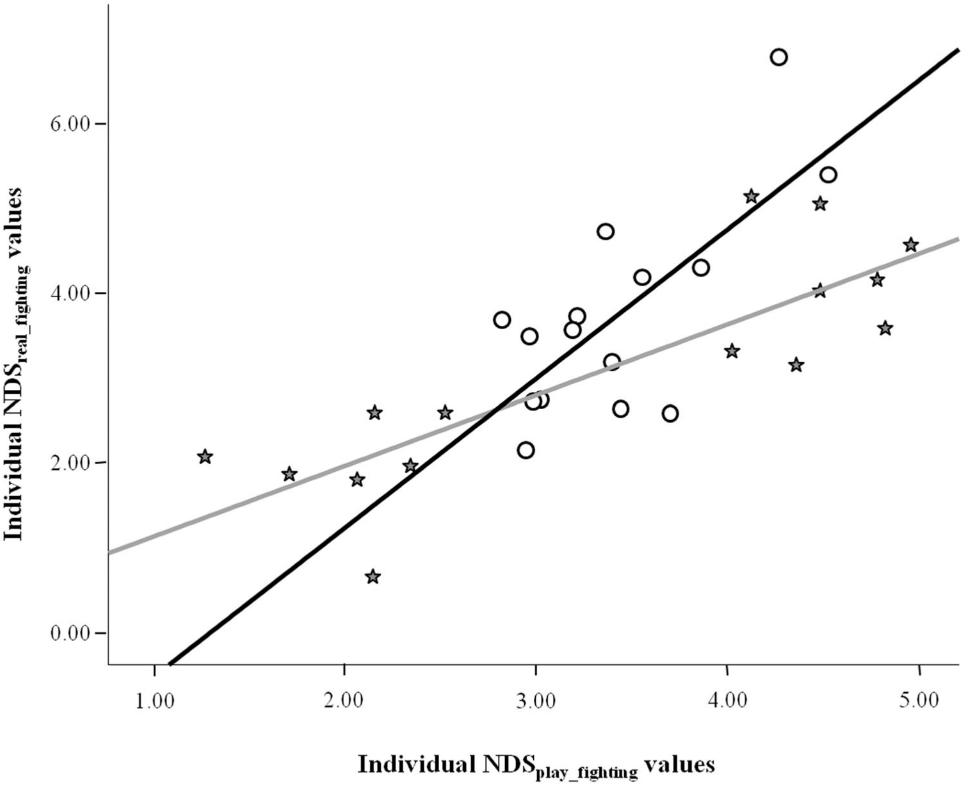

FIGURE 4 Scatter-plot showing the positive correlation between ranking positions covered by males (white circles) and females (gray stars) in real fighting ($NDS_{real\_fighting}$; Y-axis) and play fighting ($NDS_{play\_fighting}$; X-axis). NDS, Normalized David's Score.

respect on non-human primates, it has been suggested that in adult humans repetition is important for action training because movements become more stable as motor-skills improve (Barbado Murillo et al., 2017; Wynberg et al., 2021). In humans, the performance of a given activity is improved by repetition (Magallón et al., 2016; Willingham & Koroshetz, 1993). The process of acquisition and perfection of a new repertoire of movements is based on practice and induces neuronal plasticity, particularly at cerebellum level (Boyden et al., 2004; Kleim et al., 1997; Park et al., 2009). In rats, Whishaw et al. (2021) demonstrated that during play fighting adult individuals repeatedly used their hands and this was associated to motor training for the use of hands in many hand-related behaviors.

In our study colonies, play fighting sessions were more symmetrical than real fighting sessions, thus individuals reciprocated more frequently offensive and defensive patterns while playing (Figure 3). As suggested for mutual grooming, in adult chimpanzees a reciprocal and symmetric exchange of behavioral patterns (i.e., attack and defensive maneuvers) during play fighting between individuals can serve as a signal of willingness to invest in the play bout and to prolong it (*Immediate Investment Hypothesis*; Allanic et al., 2020; Machanda et al., 2014). It has been posited that in chimpanzees the proximate cause of structural and temporal changes of play are partly explained by *Heider's Balance Theory* (Heider, 1946), according to which group-member would be motivated to change their unbalanced social interactions (in terms of reciprocity) into balanced ones to prolong these interactions (de Nooy et al., 2005; Krackhardt & Handcock, 2007; Moody, 2009; Shimada, 2013). Play fighting in adult chimpanzees can result as a blend of competition and cooperation (Pellis et al., 2010, 2022) that have to always maintain a certain grade of reciprocity to allow the "non-serious" interaction to continue. Thus, in adult chimpanzees symmetry (i.e., reciprocity in offensive and defensive behavioral pattern exchange) may be a key-structural-feature that characterizes play fighting although different primate and non-primate species may incorporate reciprocity in different ways (Bauer & Smuts, 2007; Cordoni et al., 2016, 2018, 2021; Pellis et al., 1993; Pellis et al., 2022).

Repetition and symmetry may work in prolonging the play session. Accordingly, we found that play fighting sessions lasted longer and were composed of more behavioral patterns (an indirect indicator of session length) than real fighting sessions. Indeed, in both primate and non-primate mammals play is supposed to be a pleasurable and rewarding activity, which would lead to its prolongation (Burghardt, 2011; Held & Špinka, 2011; Pellis et al., 2014; van Kerkhof et al., 2013). From a functional point of view, the duration can be a reliable measure of play success because - by prolonging their interactions—individuals have more time for social assessment (Bertini et al., 2021; Palagi et al., 2019). In the long-term perspective, the period of time two subjects interact may shape the quality of their relationship (Hinde, 1979). Because chimpanzees invest in affiliative relationships throughout their lives and use play as social currency (Bray et al., 2021; Koski et al., 2012; Rosati et al., 2020; Schroepfer-Walker et al., 2015), we can assume that longer play-fighting sessions can represent a valuable currency for social bond formation and maintenance.

Even though symmetry was higher in play fighting sessions compared with real fighting ones, such symmetry did not imply a dominance-reversal during play. On the contrary, in the current study, both females and males maintained their ranking positions across contests (i.e. play and aggression). Hence, from a parsimonious point of view, we can hypothesize that in adult chimpanzees dyadic dominance relationships are translated from real fighting into play fighting. We can also suggest that play fighting has a highly competitive nature and can possibly replace aggression under certain circumstances (Cordoni et al., 2021; Paquette, 1994).

5 | CONCLUSIONS

Overall, our results evaluated in a quantitative and replicable way that session duration and behavior repetition and symmetry can be key features of play fighting in adult chimpanzees whereas role-reversal and behavior variability and distribution uniformity cannot be. We can suggest that play fighting in adult chimpanzees may have elements of serious context (i.e., real fighting) such as the absence of role-reversal. To our knowledge few studies have identified play as a possible (and safe) substitute for aggression (Cordoni et al., 2021; Paquette, 1994) or as a way to determine and/or maintain dominance relationships (Yamanashi et al., 2018) in chimpanzees. We may expect that also in immature chimpanzees play can include elements of serious context and can be competitive for obtaining benefits that partly overlap with those obtained by adult individuals (e.g., anxiety reduction, social assessment). In this view, we can suppose that play may be not always an indicator of positive animal welfare. Future research works are needed to investigate playful interaction structure and manifestation in a nuanced way with respect to facial expressions, individual/group features, and socio-environmental context so to better understand the motivation that underlies what appears to be play or rather motivational changes (e.g., from playful to aggressive) during sessions.

AUTHOR CONTRIBUTIONS

Giada Cordoni: Conceptualization (lead); data curation (equal); formal analysis (lead); methodology (lead); supervision (lead); writing—original draft (lead); writing—review & editing (lead). **Giulia Ciarcelluti**: Data curation (equal); formal analysis (supporting). **Altea Pasqualotto**: Data curation (equal); formal analysis (supporting). **Annarita Perri**: Data curation (equal); formal analysis (supporting). **Veronica Bissiato**: Data curation (equal); formal analysis (supporting). **Ivan Norscia**: Conceptualization (lead); data curation (equal); formal analysis (lead); methodology (lead); supervision (lead); writing—original draft (lead); writing—review & editing (lead).

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CONFLICTS OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available in the supplementary material of this article.

ETHICS STATEMENT

The current study was purely observational and non-manipulative, thus approval was not required by the authors' institutional animal care committees. The study adhered to both the American Society of Primatologists Principles for the Ethical Treatment of non-human primates and legal requirements of the country in which the research was conducted.

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