Play contagion in African elephants: The closest, the better

Ivan Norscia [a],[*],[1], Martin Hecker [a], Beatriz Gallego Aldama [b], Santiago Borragán Santos [b], Giada Cordoni [a],[*],[2]

[a] Department of Life Sciences and Systems Biology, University of Torino, Italy
[b] Cantur, S.A. Parque de la Naturaleza de Cabárceno 3, Obregón, Cantabria 9690, Spain

ARTICLE INFO

ABSTRACT

Behavioural contagion is an automatic process through which a behaviour performed by an individual (trigger) is reproduced by an observer (responder) without necessarily replicating the exact motor sequence. It has been linked to inter-individual synchronisation and possibly emotional contagion. Play can convey emotions and enhance social bonding, although its contagiousness is understudied. To verify social play contagion presence and modulating factors, we gathered audio-video data on social play, distance and affiliation on a group of savannah African elephants (15 individuals) at Parque de la Naturaleza de Cabarceno (Cantabria, Spain). Social play was contagious as it was more likely started by uninvolved elephants (within 3-min) in Post-Play Condition (PP) - after that other elephants had started playing - than in Matched-control Condition (MC; no previous play). Social play contagion mostly occurred within 30 m – probably due to elephants' limited visual acuity – and it was highest between individuals that affiliated the most, with the distance-affiliation interaction having no effect. The most prominent individuals in the social play network were also the most influential in the play contagion network (Eigenvector-centrality measure). Play contagion was socially modulated, thus suggesting it may extend from motor replication to the replication of the underlying affective state.

1. Introduction

Behavioural matching occurs when an individual performs the same behaviour (hereafter 'target behaviour') that another individual is enacting or has just enacted (Gallese, 2003; Schütz-Bosbach and Prinz, 2015; Zentall, 2003). Behavioural matching has important repercussions on social life in that it can promote cooperation, emotional sharing and social learning (Berthier and Semple, 2018; Canteloup et al., 2020; Panksepp and Panksepp, 2013; Paukner et al., 2009). It is a multifaceted phenomenon that involves the replication of others' actions in different conditions (and cognitive complexity): i) implicitly when both the trigger and the action are observed ('*automatic motor mimicry*' or '*behavioural contagion*'; Wheeler, 1966; Zentall, 2003); ii) in presence of the trigger, with no observation of the target behaviour (*mere presence*; Hoppitt and Laland, 2008); iii) in presence of the object, with no observation of the trigger ('*learned affordances*' or '*stimulus enhancement*', depending on whether the target behaviour is triggered by object learned features or movement, respectively; Zentall, 2003; 2012); iv)

when the goal of trigger's action is understood ('*true imitation*'; Huber et al., 2009; Carpenter et al., 2002).

Behavioural contagion (Wheeler, 1966; Zentall, 2003) and automatic motor mimicry (sometimes labelled as 'imitation'; Simpson et al., 2014) are basic forms of behavioural matching that occur when an individual observes others' motor patterns and implicitly replicates them within seconds (mimicry) or minutes (contagion; Iacoboni, 2009; Palagi et al., 2020; Schütz-Bosbach and Prinz, 2015; Zentall, 2003). Via the Perception-Action Mechanism (PAM) and the Mirror Neuron System (MNS), the same motor neurons that are activated in the trigger (that actually performs the action) can be automatically primed in the observer, with the action goal being more relevant than the motor pattern *per se* (MNS; Rizzolatti and Fabbri-Destro, 2010; Schütz-Bosbach and Prinz, 2015) and with the response being influenced by the observer's experience (PAM; de Waal and Preston, 2017; Preston and de Waal, 2017). According to some definitions, behavioural contagion differs from mimicry in that it does not require the replication of the exact motor pattern (Wheeler, 1966; Zentall, 2003). Mimicry and

---

contagion may allow shared representations and may favour the establishment of an implicit bond between trigger and observer, possibly extending from motor acts to the affective states underlying such acts (de Waal and Preston, 2017; Caruana, 2019; Preston and de Waal, 2017; a summary of motor replication phenomena is included in Table 1).

Despite its importance, behavioral contagion has been understudied especially in relation to interactive social behavior. Most literature has focused on the contagion of non-interactive motor patterns, namely scratching (e.g. orangutans: Laméris et al., 2020; humans: Schut et al., 2015; spider monkeys, *Ateles geoffroyi*: Valdivieso-Cortadella et al., 2023; mice: Yu et al., 2017) and yawning (e.g., Van Berlo et al., 2020; for review: Palagi et al., 2020), which can be subject to contagion, rather than mimicry, as yawning can involve not just the mouth but also pandiculation in other body regions (e.g, stretching; Baenninger, 1997). With respect to interactive behaviour, behavioural contagion has been demonstrated in primates for social grooming (macaques, via visual cues: Berthier and Semple, 2018; Ostner et al., 2021; chimpanzees, via acoustic cues: Videan et al., 2005) and aggression, although by few studies (via acoustic cues; common marmosets, Watson and Caldwell, 2010; chimpanzees; Baker and Aureli, 1996; Videan et al., 2005).

Table 1
Summary of behavioural matching types. In bold the focus of the study. PAM: Perception-Action Model; MNS: Mirror Neuron System. (Adapted from Carpenter et al., 2002; Hoppitt and Laland, 2008; Huber et al., 2009; Iacoboni, 2009; Palagi et al., 2020; Preston and de Waal, 2017; Schütz-Bosbach and Prinz, 2015; Rizzolatti and Fabbri-Destro, 2010; de Waal and Preston, 2017; Wheeler, 1966; Zentall, 2003, 2012).

Phenomenon	Definition	Types (from more to less basic)	Definition
Behavioural matching	General phenomenon that refers to an individual (responder) that replicates the behaviour (target behaviour) enacted by another individual (trigger)	**Automatic replication** (possibly associated with emotional contagion, when it extends from the replication of motor acts to the replication of the affective states underlying such acts, e.g. via PAM/MNS)	Motor mimicry: replication within seconds that occurs when both trigger and motor pattern are observed and the same motor pattern is replicated (e.g. smile mimicry) **Behavioural contagion**: replication within seconds or minutes that occurs when both trigger and motor pattern are observed but it does not always involve the use of the same motor patterns (e.g. yawn contagion). It may involve high order, articulated, behaviours (e.g. **play contagion**).
		Mere presence	Replication that occurs in presence of the trigger, with no observation of the target behaviour
		Learned affordances/ stimulus enhancement	Replication that occurs in presence of the object, with no observation of the trigger
		True imitation	Replication that occurs when the goal of target behaviour is understood

Different individual factors – such as age, rank, and sex - may affect behavioural contagion. Age can affect behavioural contagion – specifically yawn contagion - in some cohorts of human and non-human animals (humans: Anderson and Meno, 2003; Bartholomew and Cirulli, 2014; Helt et al., 2010; Hoogenhout et al., 2013; chimpanzees, Madsen et al., 2013; bonobo: Norscia et al., 2022; domestic pigs: Norscia et al., 2021b), with contagion possibly increasing in the immature phase up to adulthood (followed by a subsequent decrease with aging). Scratching and yawn contagion – however – did not appear to be affected by age for example in howler monkeys (*Ateles geoffroyi*; Valdivieso-Cortadella et al., 2023). To our knowledge no information on age effect is available for the contagion of interactive behaviour. Other than age, also sex may influence - in a variable way - behavioural contagion (namely, yawn contagion and scratching), although such influence is not consistent across different cohorts of individuals and species in human and non-human primates (cf. Bartholomew and Cirulli, 2014; Chan and Tseng, 2017; Demuru and Palagi, 2012; Norscia et al., 2021a; Valdivieso-Cortadella et al., 2023). Moreover, the effect of rank has been hypothesised for the contagion of non-interactive behaviour (i.e. yawn contagion) in relation to the individuals of the dominant sex (possibly eliciting more responses; e.g. in male chimpanzees; Massen et al., 2012) and was found for grooming in macaques (where the latency of the grooming response was affected; Ostner et al., 2021).

Perceptual factors can also influence behavioural contagion. Indeed, a crucial aspect of behavioural contagion is that both the trigger and the action are perceived by a potential responder so as to activate a shared representation leading to action replication (de Waal and Preston, 2017; Zentall, 2003). Thus, distance may affect behavioural contagion (e.g. yawn contagion) especially in open spaces when visual acuity is scarce (Norscia et al., 2021b).

Finally, social factors such as group membership and social bonding can affect behavioural contagion. In particular, group membership can bias behavioural contagion (i.e. yawn contagion) and/or rapid mimicry in humans and non-human animals, although not always in a consistent way (e.g., mimicry: Bagnis et al., 2019; Bourgeois and Hess, 2008; yawn contagion; chimpanzees: Campbell and de Waal, 2011; geladas: Gallo et al., 2021; bonobos: Tan and Hare, 2017). Additionally, in human and non-human animals, mimicry and behavioural contagion (i.e. yawn contagion) can be positively affected by prosociality, social bonding and affiliation levels (e.g. human mimicry: Leighton et al., 2010; play face rapid mimicry in dogs: Palagi et al., 2015; yawn contagion; humans: Norscia and Palagi, 2011, Norscia et al., 2020, 2021; bonobos: Demuru and Palagi, 2012; red-capped mangabeys: Pedruzzi et al., 2022; domestic pigs: Norscia et al., 2021b; but see Norscia et al., 2022 and De Vittoris et al., 2024 for bonobos).

Acoustic and visual play cues can elicit social play but quantitative studies demonstrating play contagion are scarce (e.g. rats: Pellis and McKenna, 1992; Varlinskaya et al., 1999; kea parrots: Schwing et al., 2017; ravens: Wenig et al., 2021; Osvath and Sima, 2014). Social play contagiousness could be adaptive, as in mammals it can reduce the anxiety linked to high social tension contexts in the short term (e.g. Cordoni and Palagi, 2007; Palagi et al., 2004; Norscia and Palagi, 2011) and favour physical, cognitive and emotional development in the long term (Fagen, 1993; Pellis et al., 2010; Pereira and Fairbanks, 2002; Spinka et al., 2001). By using Social Network Analysis it is possible to check for the centrality of individuals in the relations with others, including either actual interactions or possible 'immaterial relations' such as contagion (Cherven, 2015; Norscia et al., 2022; Saqr et al., 2018).

Here, we quantitatively investigated whether social play was contagious in a captive colony of savannah African elephants (*Loxodonta africana*). African elephants live in multilevel societies with family units composed of kin females and offspring and they are a good model to investigate this issue because they show a wide array of social play patterns, used to socialize with peers and establish long-term relationships (Lee, 1987; Lee and Moss, 2014; Raviv et al., 2023). Based on the

above framework and on elephant biology we formulated the following predictions.

1.1. Prediction 1 – Presence of social play contagion

Social play can be elicited by the exposure to play cues or the observation of others playing (e.g., Pellis and McKenna, 1992; Schwing et al., 2017; Wenig et al., 2021). Social play in African elephants has a high adaptive value as it contributes to maintain the high tolerance levels typical of the species and possibly reflect a self-domestication process (Raviv et al., 2023). Hence, we expected that social play could be contagious in savannah African elephants and that individuals (hereafter, responder) would be more likely to start playing after that others (hereafter, triggers) began playing (Prediction 1).

1.2. Prediction 2 – Social play and social play contagion networks

In mammals, individuals can greatly differ in the play rates as a function of several variables, including individual personality (e.g. rats: Pellis and McKenna, 1992; Siviy et al., 2011; elephants: Webber and Lee, 2020; macaques: Wright et al., 2018). Moreover, when an individual approaches another to play and start play patterns, the recipient may respond by engaging in play or not (Cordoni et al., 2021; Cordoni and Palagi, 2011).

Similarly, in elephants play can occur at variable rates and may be especially revealing of internal states or emotion (Lee and Moss, 2014; Webber and Lee, 2020). Hence, we expected that the individuals showing highest propensity to engage in play – thus being central in the network of social play – could also be more sensitive to be affected by the play mood of others, thus being also central in the network of social play contagion.

1.3. Prediction 3 – Factors modulating social play contagion

Age may affect behavioural contagion (and specifically yawn contagion) – which may increase with age – although the age effect has not always been consistently found and direct frequency comparisons across age classes are scarce (e.g., Anderson and Meno, 2003; Bartholomew and Cirulli, 2014; Norscia et al., 2021b; De Vittoris et al., 2024) In elephants (both African and Asian species) social play is largely observed in calves and juveniles and persists into adulthood (Lee and Moss, 2014; Lee, 1987; Raviv et al., 2023). Hence, we did not expect social play contagion – if present – to be affected by age (Prediction 3a). Depending on the species and cohorts of individuals, sex has been found to affect or not contagious behaviour (yawn contagion and scratching cf. Demuru and Palagi, 2012; Norscia et al., 2022; Bartholomew and Cirulli, 2014; Chan and Tseng, 2017). The literature indicates some qualitative differences between males and females in social play but no considerable differences in frequencies (Lee and Moss, 2014). Hence, we predicted that the social play would not differ between sexes (Prediction 3b).

Rank may affect behavioural contagion but literature in this respect is limited (Madsen et al., 2013; Ostner et al., 2021). African elephants show an age-dependent hierarchy but they are characterized by increased tolerance levels and low aggression rates, with social play mostly involving immature subjects with either peers or adults (Raviv et al., 2023; Wittemyer and Getz, 2007). Thus, we did not expect dominance rank to affect social play contagion (Prediction 3c).

Behavioural contagion can be affected by distance especially in open spaces when visual acuity is scarce (e.g. yawn contagion in pigs; Norscia et al., 2021b). Because African elephants possess a moderate degree of visual acuity (Pettigrew et al., 2010), we expected that an increased distance between the trigger and the possible responder – by affecting the likelihood of detecting the target behaviour – would reduce the probability of contagion (Prediction 3d).

Group membership may variably bias behavioural contagion (e.g., yawn contagion; chimpanzees: Campbell and de Waal, 2011; geladas:

Gallo et al., 2021; bonobos: Tan and Hare, 2017). In Savannah African elephants, individuals are part of fission-fusion multi-tiered society characterized by a continuum of social interactions and affiliation levels are not always predicted by kinship, as females also affiliate with non-kin (Wittemyer et al., 2005; Archie et al., 2011). Consistently, the same group considered in this study, Norscia et al. (2024) found that affiliation levels were comparable within and between families. Moreover, juveniles engage in social play both within and outside their family to socialise with peers (Lee, 1987; Raviv et al., 2023;). Hence, we expected that family membership would not significantly affect social play contagion (Prediction 3e).

Finally, in human and non-human animals, strong social bonding and affiliation may enhance mimicry and behavioural contagion (e.g., Leighton et al., 2010; Norscia et al., 2021b; Norscia and Palagi, 2011, Demuru and Palagi, 2012; Palagi et al., 2015; Pedruzzi et al., 2022; Norscia et al., 2021a). Because elephants extensively use social play to build social bonds also with non-kin (Raviv et al., 2023; Lee and Moss, 2014), we expected that higher level of non-playful affiliation between individuals may enhance social play contagion (Prediction 3 f).

2. Methods

2.1. Study site and colony

This research was conducted on a colony of 15 African savanna elephants (*Loxodonta africana*) housed at the Parque de la Naturaleza de Cabárceno (Santander, Cantabria, Spain), in a natural habitat outdoor space of 25 ha. The elephants would remain outdoor the whole day and would spend the night indoor. The colony was composed of: six immature subjects (2–5 years old, two females and two males; a 10 years old male and a 11 years old female at pre-pubertal stage), two late adolescents (two females, 17 and 19 years old), and seven adults (two males and five females, 21–45 years old (age classes *as for* Evans and Harris, 2008). In the colony, family units were composed by the matriarch, kin-related females and offspring. Colony information (individual identity, age, sex, and kinship) is reported in Table 2. Several elevated viewpoints permitted the observations of most or all elephants, outdoor.

2.2. Data collection and operational definitions

Behavioural data were collected outdoor on a daily basis (4–6 days/week) from April 2022 to July 2022, from 9:00–18:00 hrs (with morning/afternoon shifts). Observations were carried out live and with the support of full HD audio-videos (via Panasonic HC-V180). Via all occurrences sampling methods, on the visible individuals, we collected

Table 2
Identity, age, sex, and kinship in the study group.

Individual	Sex	Age	Father (in the colony)	Mother (in the colony)	Offspring
Jums	M	45			
Penny	F	42			
Zambi	F	41			Kenia, Infinita
Kira	F	27		Penny	Africa (Pamba)
Kenia	F	21		Zambi	
Infinita	F	17		Zambi	Toranzo
Brisa	F	19			Toribio
Hilda	F	21			Martin, Saja, Maruca
Africa (Pamba)	F	11		Kira	
Toranzo	M	4	Jumar	Infinita	
Toribio	M	4	Jumar	Brisa	
Saja	F	5	Jumar	Hilda	
Maruca	F	2	Jumar	Hilda	
Martin	M	10	Jums	Hilda	
Jumar	M	25	Jums		

data on social play, agonistic contacts and subordination patterns (to calculate dominance rank as explained below), and affiliation behavioural bouts. We extracted 30 hours of dyadic social play videos out of 91 hours of video footage. The ethogram used for this study is summarised in Table 3. For each social behaviour session we recorded the actor (the individual starting the action) and the receiver (the recipient of the action).

We applied a modified version of the Post-Conflict/Matched Control (PC-MC) method, originally defined to assess post-conflict reunions in animals (de Waal and Yoshihara, 1983) and more recently used to verify the presence of grooming and yawn contagion (Berthier and Semple, 2018; Norscia et al., 2022; Ostner et al., 2021). We defined two main conditions: (1) Post-Play (PP) and (2) Matched Control (MC). In the PP-condition, we considered the actor - that is the first subject that started a social play (*as per* Table 3) with another subject (receiver) - and marked such subject as 'trigger'. The beginning of the trigger behaviour was marked as the start time (t_0) of the 3-min post-trigger observation period. To reduce possible confounding variables, PP (t_0) started only after 3 full minutes without social interactions. In case of behavioural chains (a sequence of repeated bouts of the same target, play behaviour separated by at least 30 s) within the 3-min period, the last one of the play sessions was considered as the trigger behaviour. The other visible subjects were considered as 'potential responders' that is subjects that could perform the same target behavior enacted by the trigger (hereafter referred to as 'response behaviour'). Their behaviour was recorded in the 3-min following the start time to verify whether there was a behavioural response (start of social play) or not. It was also recorded whether the potential responders were within 30 m or not from the trigger. Subjects were excluded from the set of potential responders when they received direct play invitation patterns (Table 3), were already involved in the trigger behaviour, solitary play or other social behaviours during the PP. In the Matched Control (MC)— the same potential responders were observed for three minutes - at the same time (±1 h) as the PP on another suitable day - to check whether they were involved in a social play session. The MC observation was carried out under similar social and environmental conditions (e.g. same weather, presence of a similar number of individuals within and/or beyond 30 m) and in the absence of any previous social play session. In both conditions, the trigger and response behaviour was recorded in absence of external perturbing events to reduce the probability that the response behaviour could be triggered by an external stimulus rather than being elicited by the trigger behaviour itself. We collected 157 PP-MC pairs. For each 3-min period, PP-MC pairs were defined as: (i) attracted (APs) if social play occurred in PP and not in MC; (ii) dispersed (DPs) if social play occurred in MC and not in PP; (iii) neutral (NPs) if social play occurred in both PP and MC conditions (or neither of them). Based on the method of calculation of the Corrected Conciliatory Tendency (de Waal and Yoshihara, 1983; Veenema et al., 1994), we calculated the Individual Play Contagion Tendencies (IPCTs) as follows: (APs − DPs)/(APs + DPs + NPs).

To reduce observation biases, dyadic behavioural frequencies of affiliation were obtained by weighting the affiliation bouts over the number of observation hours of the interacting dyad (the time both the individuals of a given dyad were seen together).

Behavioural coding was carried out by M.H. after a training with I.N. and G.C., and the training ended when the inter-observer reliability measured via Cohen's k reached 0.80 for both social play and affiliation behaviours (good agreement; *sensu* McHugh, 2012).

2.3. Social networks

Via freeware Gephi 0.9.7 (www.https://gephi.org/, distributed under the dual license CDDL 1.0 and GNU General Public License v3; Cherven, 2015), we determined Social Play Network (SPN) and social Play Contagion Network (PCN), both including the network actors (nodes) and the relations between them (edges). In particular, the social

Table 3
Social play ethogram used for data collection (as per Norscia et al., 2024; modified from Langbauer, 2000; Lee and Moss, 2014; Lefeuvre et al. 2020; Poole and Granli, 2011; Webber and Lee, 2020; Wilson, et al., 2006).

Pattern	Description
AFFINITIVE BEHAVIOURS	
Affinitive contact patterns	This item involves the following: i) Contact/nudge: an elephant stays in physical contact (or sits on) with another elephant making contact with at least part of the body (head-head, head-body or body-body, etc.) (not including touching with trunk); ii) social rub: an elephant rubs a part of its body against a fellow's body; iii) tail: an elephant holds the tail of another elephant with the trunk or underneath a leg; iv) push/pull under: an adult elephant pushes or pulls a calf under its belly; v) climb: an elephant places at least one foot on top of another elephant, usually one that is lying down; vi) gather: elephants gather together in a close cluster pressing their bodies against one another
Affinitive non contact patterns	This item involves the following: i) proximity: an elephant stays at ≤1 elephant body length distance from another elephant; ii) parallel walk: two elephants walk side by side with no aggressive behaviour for 3 or more steps; iii) follow: an elephant walks closely behind (within 2 elephant body lengths) of another elephant: iv) lean: an elephant leans on another elephant; v) stand over: an elephant stands close to another, watching toward the other; iv) back toward: an elephant turns to present posterior and walks slowly backwards into another individual; the pattern can be accompanied by vocalisation.
Suckling related patterns	This item involves the following: i) solicit suckling: an infant calf calls to the mother for milk, walks parallel to the mother and can push the mother against her legs, push the trunk near to the teat, place the trunk around the mother's leg and/or touch her nipples; ii) suckling: an infant suckles from the mother's teat and the mother lifts her trunk back over the infants head to allow the infant to access to the teat with their mouth
Trunk contact patterns	This item involves the following: i) touch: an elephant touches another elephant, not the mouth or genitals, with the trunk in absence of aggressive behaviour; ii) caress: an elephant uses the trunk to touch another; iii) envelope: an elephant wraps a body part of a fellow with its trunk; iv) lifting: an elephant stretches out its trunk and raises it towards an approaching individual; v) mouth: an elephant puts the trunk in the mouth of another elephant; vi) two elephants intertwine their trunks
SOCIAL PLAY BEHAVIOURS	
Social play contact patterns:	This item includes the following: i) American football: elephants try to catch an object by play fighting (e.g. pushing aside, pulling) with one or more fellows; ii) clamber: elephants clamber onto others forming a pile of wriggling, squirming elephants, iii) kneel-down: an elephant lowers himself down on his knees and playfully spars with a smaller partner; iv) play mock charge: an elephant withdraws and then runs towards the fellow and pushes it; v) play push: an elephant exerts force on a fellow with a part of its body while performing other behaviours coded as play; vi) retrieve: an elephant pulls back another with its trunk; vii) play slap: an elephant hits another with its trunk; viii) play sparring: two elephants engage into head-to-head contact; ix) play trunk wrestle: two elephants entwine their trunks and push each other back and forth; x) tickle: an elephant stimulates another via repeated gentle contacts with its trunk (in association with at least another play pattern); xi) play fighting: two elephants engage in wrestle with no observable aggressive patterns.
Social play non-contact patterns:	This item includes the following: i) forward-trunk-swing: an elephant swings or tosses the trunk toward an adversary; ii) play run: an elephant rapidly follows another; iii) play stretching head: an elephant stretches its head down and forward while gazing at a play partner; iv) play trunk periscope: an elephant pauses and approaches a group mate with the trunk held up in a periscope or S-shape position.

Table 3 (*continued*)

AGGRESSIVE AND SUBMISSIVE BEHAVIOURS	
Aggressive contact patterns	This item includes the following: i) bite: an elephant closes its mouth on the body/trunk/tail of a conspecific; ii) kick: an elephant strikes out or hits another with its foot; iii) push/tusk: an elephant exerts force against the body of a conspecific (with body parts or tusk), resulting in the other elephant moving at least two steps; iv) slap: an elephant hits another with trunk or tail; v) charge: an elephant rushes at another with its head held high or low and its ears spread out, with the trunk held under so as that the tusks make contact first; in the mock charge the elephant can kick dirt in the direction of the adversary, swing its trunk and/or in association with shrill trumpet blast; vi) ramming: an elephant lowers its head with its trunk curled under and rushes toward another, goring or poking it with its tusks; vii) duelling: two elephants make head to head contact, with trunk pushing, tusking, shoving, wrestling or trunk entwining, in association with threat-rumble; viii) stand-off: two elephants stand facing in opposite directions with foreheads pushing against each other.
Aggressive non-contact patterns	This item includes the following: i) bush-bash: an elephant beats vegetation with the head, tusks or hind legs: ii) kick object: an elephant strikes out or hits an object with its foot; iii) head shaking: an elephant moves rapidly its head from side to side with ears flapping; iv) object throwing: an elephant lifts or uproots objects and throw them in the general direction of an opponent: v) chase: an elephant runs after another which is rapidly withdrawing; vi) ear fold: an elephant orients its head towards another elephant, flapping it, with ears extended and held out perpendicular to the head; vii) directed trunk swing: an elephant vigorously swings or tosses the trunk around in the direction of an adversary, usually while blowing forcefully out through the trunk; viii) smack: an elephant hits the trunk on the floor in an aggressive manner; ix) tusk-ground: an elephant bends or kneels down, and tusks the ground and uplifts vegetation; x) turn/advance toward: an elephant reorients its body to gaze at an opponent or engages in directed walking toward another.
Submissive/dominance patterns:	This item includes the following: i) Turn-rear: an elephant turns its rear end towards the dominant elephant or backing towards it; ii) head-low: an elephant holds its head low (so that the top is below the level of the shoulder blades) or approaches another with head low; iii) avoid: an elephant moves away when another elephant moves toward it; iv) displacement: an elephant approaches a location and this is followed by another elephants leaving that location.

networks were obtained from the number of social play interactions (SPN, directed edges: A→B if A was the play initiator and B the recipient; B→A if the other way around) and dyadic events of play contagion (PCN, directed edges: A→B if A was the trigger and B the responder; B→A if the other way around) and normalized over the dyad observation time and - to minimize the risk that more contagion could be simply related to being exposed to more play - the number of opportunities to observe contagion, respectively.

Via Social Network Analysis, we calculated the SPN and PCN Eigenvector centrality values. Eigenvector centrality measures the influence of a node by considering both its direct connections and the centrality of its neighbours. Based on these two parameters, the equation iteratively calculates the centrality of each node, and it continues until the centrality scores converge (Ruhnau, 2000). Hence, nodes with high eigenvector centrality are those that are connected to other highly central nodes in the network.

2.4. Statistical elaboration

Dominance rank was determined from a sociomatrix that included aggressive and submissive patterns via Steepness 2.2 (Leiva and De Vries, 2011). We obtained Normalized David's Scores (NDS) from the dyadic dominance index (Dij), in which the proportion of wins (Pij) is corrected for the probability that the observed outcome occurs. Such probability is computed on the basis of a binomial distribution, with the assumption that each individual has an equal chance of being the winner or the loser of each agonistic interaction (de Vries et al., 2006).

To test prediction 1 (presence of play contagion), we applied the non-parametric Exact Wilcoxon signed-rank test to compare individual social play occurrences between PP and MC conditions (Mundry and Fischer, 1998; Siegel and Castellan, 1988). The non-parametric test was applied owing to non-normal distribution of social play occurrences (Kolmogorov-Smirnov test: $N_{individuals}=15$, p<0.05).

To test prediction 2 (social play and social play contagion networks), due to normal distribution of Eigenvector centrality values obtained via the SNA (Kolmogorov-Smirnov test: $N_{individuals}=15$, p = ns), we applied a Pearson's bivariate test to correlate the values between the networks of social play and social play contagion. To avoid intrinsic covariance, for this analysis we excluded the play sessions triggered via contagion.

To test prediction 3 (factors modulating play contagion), on the data collected in the PP condition we ran two Generalized Linear Mixed Models (GLMMs). We checked for the possible effect of individual, spatial and social factors on the occurrence of social play contagion. We ran a model ($GLMM_1$) considering the actor as social play trigger (first individual that started playing) and a control model ($GLMM_2$) with the same variables but replacing the actor (or trigger) with the receiver (the recipient of the first social play). In both models ($GLMM_1$ and $GLMM_2$) we defined the occurrence of social play contagion as the target variable (binomial: yes/no). We included the following fixed factors: i) actor sex, age, and rank ($GLMM_1$) or receiver sex, age, and ran ($GLMM_2$); ii) potential responder sex, age and rank; iii) distance between potential responder and the play session start spot ($GLMM_1$ and $GLMM_2$); iv) family of potential responder and either actor ($GLMM_1$) or receiver ($GLMM_2$); and v) affiliation levels between potential responder and either actor ($GLMM_1$) or receiver ($GLMM_2$). The cases where the trigger was unique were considered (in case of behavioural chains). Age (years), rank (NDS scores) and affiliation (frequency) were included as numeric variables, whereas sex (male/female), distance (within 30 m/more than 30 m), and family (same/different) were included as binomial variables. The identities potential responder and either actor ($GLMM_1$) or receiver ($GLMM_2$) were included as random factors.

We fit the GLMMs in R via the function "glmer" of the R-package lme4 (Bates et al., 2015). We compared the full model including all fixed factors with the null model that only including the random factors (Forstmeier and Schielzeth, 2011). We used a likelihood ratio test (Dobson and Barnett, 2018) to test the comparison significance (ANOVA with argument 'Chisq'). We calculated the p values for the individual predictors based on likelihood ratio tests between the full and the null model by using the R-function "drop1" (Barr et al., 2013). As the target variables were binomial, a binomial error distribution was used. We obtained the variance inflation factor (VIF) for the GLMM numeric variables via the "vif" function in R. All VIF values were > 1.00, thus indicating no collinearity. We calculated the effect size via the package "effectsize," function effectsize which returns the best effect-size measure for the provided input GLMM. For all tests the significance probability threshold was fixed at 0.05. Trend of significance are marked for $0.05 \leq p < 0.01$.

3. Results

3.1. Presence of social play contagion

It was more likely that an individual started playing after a previous play session had been started by other individuals (PP condition) in the previous three minutes than when no other session had been started (MC condition; Exact Wilcoxon's test: $N_{individuals} = 15$, T = 0, z = −2.371, p = 0.016, Fig. 1). Hence, the phenomenon of play contagion was present in the elephant study group (a sequence of social play contagion is shown
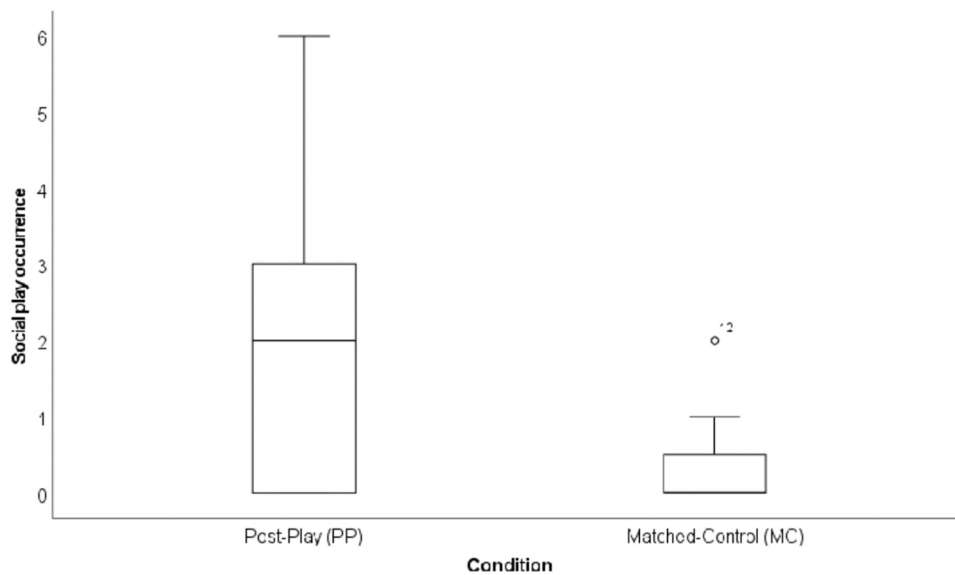
Fig. 1. Social play occurred significantly more in the Post-Play (PP) condition (after that others had started a social play session) than in the Matched-Control (MC) condition (in absence of previously started social play sessions; Exact Wilcoxon's test: $N_{individuals}$ = 15, T = 0, z = −2.371, p = 0.016).


Fig. 2. Behavioral demonstrative sequence that starts with a non-play situation (a), continues with a dyad in the foreground that has started playing and is thus engaged in a play session (b), and then concludes with a dyad in the background that has also started playing and is, therefore, also engaged in a play session (c).

in Fig. 2). IPCT ranged from −50–100 %, with the group mean ICPT = 24,37 %. Demonstration Fig. 2 and Video_S1 show an example of contagion sequence.

Supplementary material related to this article can be found online at doi:10.1016/j.beproc.2024.105092.

3.2. Social play and social play contagion networks

We found a significant correlation (Pearson's correlation: $N_{individuals}$ = 15, r = 0.614, p = 0.015) between the Eigenvector centrality values of the network of social play (Fig. 3a) and the network of social play contagion (Fig. 3b). Hence, the individuals who were more central in engaging in social play were also the most involved in play contagion.
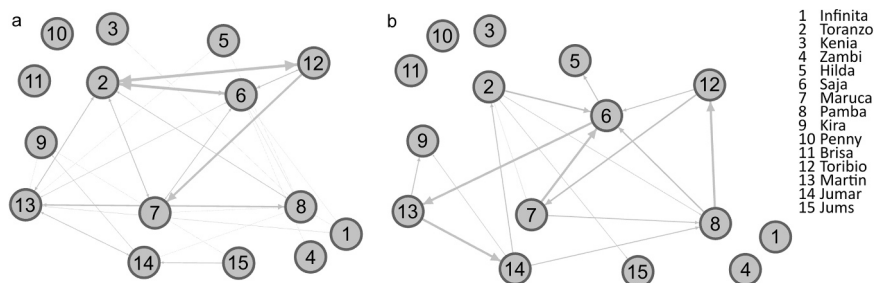
Fig. 3. Social Networks of (a) social play (excluding social play sessions elicited via contagion) and (b) social play contagion. The Eigenvector centrality values correlate between networks (Pearson's bivariate correlation: $N_{individuals}$=15, p = 0.015).

3.3. Factors modulating social play contagion

By restricting the analysis to PP data, via two GLMM$_s$ (GLMM$_1$ considering the actor, or trigger, and control GLMM$_2$ considering the receiver) we further checked what spatial, individual and social factors could influence the occurrence of play contagion. As for GLMM$_1$, the full model (including all fixed factors) and the null model (only including the random factor) significantly differed (likelihood ratio test: N$_{cases}$=164, χ^2= 29.767, df=10, p<0.001). At least one predictor had a significant effect on the target variable, hence we continued with the drop1 procedure. We found that the occurrence of social play contagion was influenced by the following variables: i) spatial distance, with social play contagion most likely to occur when the potential responder was within a distance of 30 m from the place where the first social play session took place (Fig. 4a); iii) affiliation levels, with social play contagion mostly occurring between individuals that affiliate the most (Fig. 4b). The responder's age showed a trend of significance, with younger individuals tending to start playing more often after that others had started playing. However, this factor failed to reach significance. The interaction between affiliation levels and spatial distance, and the other fixed factors, had no significant effect (complete results: Table 4).

As for GLMM$_2$, the full model (including all fixed factors) and the null model (only including the random factor) significantly differed (likelihood ratio test: N$_{cases}$=164, χ^2= 28.923, df=10, p = 0.001). Via the drop1 procedure we found that only the distance had a significant effect, with social play contagion being more contagious when the potential responder was within 30 m from the first play session spot (Table 4). No other tested variable (or variable interaction) had a significant effect. The combined results of the GLMM$_1$ and GLMM$_2$ indicate that the specific affiliation with the trigger (the first individual initiation play) and not the affiliation with the recipient of the first social play session affected contagion. The factors with a significant effect on social play contagion are shown in Table 4.

4. Discussion

Our results show that social play in savannah African elephants can be a contagious behaviour. Indeed, in our study colony, it was more likely for an elephant to start playing with group mates after that others had started playing compared to when no other elephant was playing (Prediction 1 confirmed). Indeed, play has been described as a behaviour that can be transmitted from an individual, to another (Bekoff, 2001; Fagen, 1981). For example, playback of play vocalizations were found to increase the frequency of play in keas (*Nestor notabilis*; Schwing et al., 2017). Interactive play and play with objects seem to be contagious (children: Wheeler, 1966; rats: Pellis and McKenna, 1992, Varlinskaya et al., 1999) but it may not elicit the same type of play (e.g., in ravens object play may elicit social play; Wenig et al., 2021).

Behavioural contagion is an automatic and implicit process that can 'immaterially' connect the individual that observe an action to the individual that performs such action, via shared neural representations, as predicted by the Perception Action Model (PAM) and the Mirror Neuron System (MNS; de Waal and Preston, 2017; Rizzolatti and Fabbri-Destro, 2010). The fact that social play may undergo a process of automatic inter-individual transmission is consistent with previous reports showing that social play circuitry (e.g. in rats) resides predominantly within subcortical structures, with cortical areas possibly intervening to modulate play (e.g. according to age, social partner, and in terms of complexity; for review: Siviy, 2016). In elephants play can be informative of internal states or emotion and the playful mood is variable across individuals (Lee and Moss, 2014; Webber and Lee, 2020). In our study colony, the individuals that were most central in engaging in play interactions with others (social play network) were also most involved in play contagion (social play contagion network; Prediction 2 confirmed). Because the cases of contagion were weighted over the number of occasions, this result is consistent with the possibility that the individuals who are more prone to play with others are also more sensitive to the playful mood of others.

With respect to possible modulating factors, social play contagion was affected by both spatial and social proximity (Prediction 3d and 3 f confirmed). As foreseen, the other variables did not affect social play contagion (predictions 3a-3c, and 3e confirmed). Young individuals tended to be more 'infected' by others' playful behaviour, but the effect failed to reach significance. This may be the result of the combination of two opposite trends because – on one hand - social play frequencies are maximum in the juvenile phase (Raviv et al., 2023) but – on the other hand - behavioural contagion (e.g. yawn contagion) may increase with age in certain cohorts of individuals (e.g., Anderson and Meno, 2003; Norscia et al., 2021b; Norscia et al., 2022). Such an increase may be in relation to the maturation of neural networks that elaborate social cues and the identification of others' internal states (Madsen and Persson, 2013; Norscia et al., 2021b), possibly necessary to intercept the playful internal state of others. The sex and rank of the involved individuals (trigger and responder) did not affect social play contagion either. This outcome was also expected as social play is particularly expressed in juveniles and especially between peers, with similar (low) dominance positions, as dominance is associated with age (Wittemyer and Getz, 2007). Moreover, social play is relevant to both males and females, with males mostly using it to obtain information on potential competitors and females to enhance social support with kin (Lee and Moss, 2014).

Family membership did not impact social play contagion occurrence in our study colony. Other forms of behavioural contagion, such as yawn contagion, may be enhanced either within groups as a possible form of inter-individual connection (e.g. in chimpanzees; Campbell and de Waal, 2011) or between group units for inter-group synchronisation in multilevel societies (e.g. in geladas; Gallo et al., 2021). The similar level
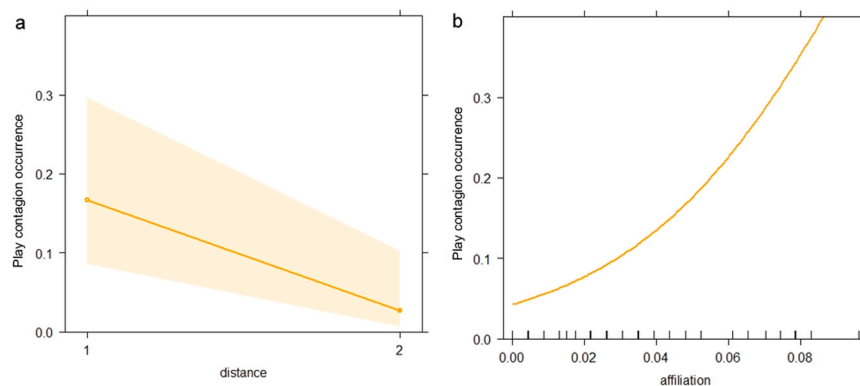

Fig. 4. Main effect of (a) distance (GLMM$_1$: χ^2 = −2.028 p = 0.043) and (b) affiliative levels (GLMM$_1$: χ^2 = 2.374, p = 0.018) between trigger and responder elephants on levels of social play contagion.

Table 4
GLMM results.

GLMM[1]	Full vs. null model: $\chi^2 = 32.666$; $df = 10$; $p < 0.001$					
(Intercept)[a]	1.014	8.830	−16.266; 18.349	a	a	a
Distance (>30 m)[b]	−2.480	1.223	−4.876; −0.083	0.027	−2.028	**0.043**
Affiliation	28.343	11.938	4.945; 51.741	0.505	2.374	**0.018**
Actor age	0.025	0.040	−0.054; 0.103	0.114	0.615	0.538
Responder age	−0.048	0.025	−0.098; 0.002	0.157	−1.898	<u>0.058</u>
Actor sex (Male)[b]	−0.883	0.679	−2.214; 0.449	0.057	−1.300	0.194
Responder sex (Male)[b]	1.125	0.714	−0.274; 2.525	0.168	1.577	0.115
Actor rank	−0.174	0.891	−1.920; 1.571	0.084	−0.196	0.815
Responder rank	−0.128	0.798	−1.692; 1.436	0.082	−0.161	0.872
Family (Same)[b]	−0.529	0.719	−1.938; 0.881	0.055	−0.735	0.462
Distance*affiliation	13.685	25.332	−35.964; 63.334	0.649	0.540	0.589
GLMM[2]	Full vs. null model: $\chi^2 = 28.923$; $df = 10$; $p < 0.001$					
(Intercept)[a]	5.879	9.101	−11.959; 23.716	a	a	a
Distance (>30 m)[b]	−3.739	1.773	−7.215; −0.263	0.030	−2.109	**0.035**
Affiliation with receiver	12.110	10.293	−8.064; 32.285	0.255	1.177	0.239
Receiver age	0.011	0.035	−0.059; 0.080	0.099	0.297	0.766
Responder age	−0.045	0.027	−0.099; 0.009	0.141	−1.639	0.101
Receiver sex (Male)[b]	−0.100	0.607	−1.289; 1.089	0.070	−0.165	0.869
Responder sex (Male)[b]	0.716	0.623	−0.506; 1.937	0.120	1.148	0.251
Receiver rank	−0.327	1.007	−2.301; 1.647	0.085	−0.325	0.745
Responder rank	−0.640	0.709	−2.029; 0.750	0.115	−0.903	0.367
Family with receiver (Same)[b]	−0.767	0.620	−1.982; 0.447	0.047	−1.238	0.216
Distance*affiliation with receiver	35.686	27.796	−18.793; 90.165	0.357	1.284	0.199

[a] Not shown as not having a meaningful interpretation

[b] These predictors were dummy-coded, with the following reference categories: Distance: ≤30 m; Actor, responder, and receiver sex: "Female"; Family and family with receiver: "Different". Significant values in bold; trend of significance: underlined.

of social play transmission with family insiders or outsiders could be linked to the fact that African elephant families are characterized by a continuum of social interactions and juveniles engage in playful interactions with both within and beyond their immediate family units as a means to test potential future rivals and establish enduring social connections (Lee, 1987; Raviv et al., 2023; Wittemyer et al., 2005).

Finally, spatial proximity (distance) and social proximity (levels of non-playful affiliation) affected the probability of social play contagion in the elephants under investigation. However, the interaction between these two factors did not produce a significant effect on social play contagion, thus indicating that these two items acted independently. In particular, spatial proximity is important as observing the triggering behaviour is primordial to then replicate it through PAM and MNS (de Waal and Preston, 2017; Gallese et al., 2004). Clearly, short distances make the detection of the triggering stimulus more likely and enhance the probability of behavioural contagion, especially in species with scarce visual acuity (as it has been observed for example in domestic pigs with yawn contagion; Norscia et al., 2021b). The influence of distance on the occurrence of social play contagion in the elephants under study is consistent with the notion that visual acuity of African elephants is moderate (approximately 4.5 times less than that of humans; Pettigrew et al., 2010).

Importantly, social play contagion in the elephants under study was influenced by the levels of non-playful affiliation that the responder had with the trigger (the actor or the first individual that initiated play). Therefore, social play contagion was not equally probable across dyads in our colony of elephants. In several other human and non-human animals, high levels of social bonding and affiliation appear to be reflected in the level of mimicry and behavioural contagion (i.e. yawn contagion) between individuals (e.g., Demuru and Palagi, 2012; Leighton et al., 2010; Norscia et al., 2021b; Norscia and Palagi, 2011; Palagi et al., 2015; Pedruzzi et al., 2022;). The asymmetrical distribution of social play contagion suggests that this form of behavioural contagion may underlie emotional contagion, the process through which emotions are transferred from an individual to another (Hess and Fischer, 2013; Preston and de Waal 2002). The automatic replication of an action or a physiological expression (e.g. motor and autonomic mimicry) can provide a physical-cognitive link between individuals that can lead them to replicate and share emotional states (Prochazkova and Kret, 2017; de Waal and Preston, 2017). According to PAM, the differences in the extent to which contagion occurs across dyads rely on the fact that shared representations develop through the observer's experience, such as memories and associations for the target, situation and state, including the relation with the trigger, which produce the inter-individual variation (de Waal and Preston, 2017; Preston and de Waal, 2017). Consistently, in the elephants under study the relationship that mattered was specifically with the elephant that showed agency in initiating play and not with any individual participating in the initial play session, as social play contagion was influenced by the affiliation levels with the trigger and not with the receiver (the recipient of the playful approach). Play contagion has been associated with the contagion of positive affective states, positively enhancing play motivation along with the emotional state of others (Held and Špinka, 2011; Špinka, 2012; Hammond et al., 2019) even though this may not always be the case (Ahloy-Dallaire et al., 2018; Adriaense et al., 2020; Größbacher et al., 2020). In savannah African elephants, different quality of social relationships are largely built upon play between juveniles and play also occurs in adulthood as a possible non-risky way of interacting (Raviv et al., 2023; Lee and Moss, 2014). It is therefore possible that the playful mood is especially transmitted and shared between closely bonded individuals, as a form of inter-individual emotional tuning.

Future studies may investigate the issue in other colonies – possibly also in the wild - and tackle in-depth play signals and patterns that are more likely to elicit or be subject to replication, as so to check whether motor mimicry can also occur in savannah African elephants.

Funding

Ethical Statement

This study is purely observational and non-manipulative, so no approval was not required from the authors' institutions.

CRediT authorship contribution statement

Giada Cordoni: Writing – review & editing, Supervision, Methodology, Formal analysis, Data curation, Conceptualization. **Santiago Borragán Santos:** Writing – review & editing, Resources. **Beatriz Gallego Aldama:** Writing – review & editing, Resources. **Martin Hecker:** Writing – review & editing, Data curation. **Ivan Norscia:** Writing – review & editing, Writing – original draft, Supervision, Methodology, Funding acquisition, Formal analysis, Data curation, Conceptualization.

Declaration of Competing Interest

Data availability

Data will be made available on request.

Acknowledgements

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.beproc.2024.105092.

References

Adriaense, J.E.C., Koski, S.E., Huber, L., Lamm, C. 2020. Challenges in the comparative study of empathy and related phenomena in animals. Neuroscience & Biobehavioral Reviews, 112, 62-82. https://doi.org/10.1016/j.neubiorev.2020.01.021.

Ahloy-Dallaire, J., Espinosa, J., Mason, G., 2018. Play and optimal welfare: Does play indicate the presence of positive affective states? Behav. Process. 156, 3–15. https://doi.org/10.1016/j.beproc.2017.11.011.

Anderson, J.R., Meno, P., 2003. Psychological influences on yawning in children. Current psychology letters. Current Psychology Letters Behavior, Brain, and Cognition, 11. https://doi.org/10.4000/cpl.390.

Archie, E.A., Moss, C.J., Alberts, S.C., 2011. Friends and relations: kinship and the nature of female elephant social relationships. In: Moss, C.J., Croze, H., Lee, P.C. (Eds.), The Amboseli elephants: A long-term perspective on a long-lived mammal. University of Chicago Press, Chicago (IL), pp. 238–245.

Baenninger, R., 1997. On yawning and its functions. Psychon. Bull. Rev. 4, 198–207. https://doi.org/10.3758/BF03209394.

Bagnis, A., Celeghin, A., Mosso, C.O., Tamietto, M., 2019. Toward an integrative science of social vision in intergroup bias. Neurosci. Biobehav. Rev. 102, 318–326. https://doi.org/10.1016/j.neubiorev.2019.04.020.

Baker, K.C., Aureli, F., 1996. The neighbor effect: Other groups influence intragroup agonistic behavior in captive chimpanzees. Am. J. Primatol. 40 (3), 283–291. https://doi.org/10.1002/(SICI)1098-2345(1996)40:3<283::AID-AJP5>3.0.CO;2-U.

Barr, D.J., Levy, R., Scheepers, C., Tily, H.J., 2013. Random effects structure for confirmatory hypothesis testing: Keep it maximal. J. Mem. Lang. 68 (3), 255–278. https://doi.org/10.1016/j.jml.2012.11.001.

Bartholomew, A.J., Cirulli, E.T., 2014. Individual variation in contagious yawning susceptibility is highly stable and largely unexplained by empathy or other known factors. PloS One 9 (3), e91773. https://doi.org/10.1371/journal.pone.0091773.

Bates, D., Mächler, M., Bolker, B., Walker, S., 2015. Fitting linear mixed effects models using lme4. J. Stat. Softw. 67, 1–48. https://doi.org/10.18637/jss.v067.i01.

Bekoff, M., 2001. The evolution of animal play, emotions, and social morality: on science, theology, spirituality, personhood, and love. Zygon® 36 (4), 615–655. https://doi.org/10.1111/0591-2385.00388.

Berthier, J.M., Semple, S., 2018. Observing grooming promotes affiliation in Barbary macaques. Proc. R. Soc. B 285 (1893), 20181964. https://doi.org/10.1098/rspb.2018.1964.

Bourgeois, P., Hess, U., 2008. The impact of social context on mimicry. Biol. Psychol. 77, 343–352. https://doi.org/10.1016/j.biopsycho.2007.11.008.

Campbell, M.W., de Waal, F.B.M., 2011. Ingroup-outgroup bias in contagious yawning by chimpanzees supports link to empathy. PLoS One 6, e18283. https://doi.org/10.1371/journal.pone.0018283.

Canteloup, C., Hoppitt, W., van de Waal, E., 2020. Wild primates copy higher-ranked individuals in a social transmission experiment. Nat. Commun. 11 (1), 459. https://doi.org/10.1038/s41467-019-14209-8.

Carpenter, M., Call, J., Tomasello, M., 2002. Understanding "prior intentions" enables two–year–olds to imitatively learn a complex task. Child Dev. 73 (5), 1431–1441. https://doi.org/10.1111/1467-8624.00481.

Caruana, R., 2019. Friends Don't Let Friends Deploy Black-Box Models: The Importance of Intelligibility in Machine Learning. Assoc. Comput. Mach. https://doi.org/10.1145/3292500.3340414.

Chan, M.H., Tseng, C.H., 2017. Yawning detection sensitivity and yawning contagion. , 2041669517726797 i-Perception 8 (4). https://doi.org/10.1177/2041669517726797.

Cherven, K., 2015. Mastering Gephi network visualization. Packt Publishing Ltd. ISBN 9781783987344.

Cordoni, G., Palagi, E., 2007. Response of captive lowland gorillas (Gorilla gorilla gorilla) to different housing conditions: Testing the aggression-density and coping models. J. Comp. Psychol. 121 (2), 171–180.

Cordoni, G., Palagi, E., 2011. Ontogenetic trajectories of chimpanzee social play: similarities with humans. PLoS One 6 (11), e27344. https://doi.org/10.1371/journal.pone.0027344.

Cordoni, G., Gioia, M., Demuru, E., Norscia, I., 2021. The dark side of play: play fighting as a substitute for real fighting in domestic pigs (Sus scrofa). Anim. Behav. 175, 21–31. https://doi.org/10.1016/j.anbehav.2021.02.016.

Demuru, E., Palagi, E., 2012. In bonobos yawn contagion is higher among kin and friends. PLoS One vol. 7 (11), e49613. https://doi.org/10.1371/journal.pone.0049613.

Dobson, A.J., Barnett, A.G., 2018. An introduction to generalized linear models. CRC press, Boca Raton. ISBN 9781138741515.

Evans, K.E., Harris, S., 2008. Adolescence in male African elephants, Loxodonta africana, and the importance of sociality. Anim. Behav. 76 (3), 779–787. https://doi.org/10.1016/j.anbehav.2008.03.019.

Fagen, R., 1981. Animal Play Behavior. Oxford University Press, New York. ISBN 9780195027600.

Fagen, R., 1993. The Pawless papers. Robert Fagen Library of Congress Cataloguing in Publication Data. ISBN 0-914061-33.

Forstmeier, W., Schielzeth, H., 2011. Cryptic multiple hypotheses testing in linear models: overestimated effect sizes and the winner's curse. Behav. Ecol. Socio 65 (1), 47–55. https://doi.org/10.1007/s00265-010-1038-5.

Gallese, V., 2003. The roots of empathy: the shared manifold hypothesis and the neural basis of intersubjectivity. Psychopathology. https://doi.org/10.1159/000072786. PMID: 14504450.

Gallese, V., Keysers, C., Rizzolatti, G., 2004. A unifying view of the basis of social cognition. Trends Cogn. Sci. (Regul. Ed.) 8 (9), 396–403. https://doi.org/10.1016/j.tics.

Gallo, A., Zanolini, A., Caselli, M., 2021. First evidence of yawn contagion in a wild monkey species, 2021, Sci. Rep. vol. 11 (1), 17957. https://doi.org/10.1038/s41598-021-96423-3.

Größbacher, V., Lawrence, A.B., Winckler, C., Špinka, M., 2020. Negative play contagion in calves. Sci. Rep. 10 (1), 21699 https://doi.org/10.1038/s41598-020-78748-7.

Hammond, T., Bombail, V., Nielsen, B.L., Meddle, S.L., Lawrence, A.B., Brown, S.M., 2019. Relationships between play and responses to tickling in male juvenile rats. Appl. Anim. Behav. Sci. 221, 104879 https://doi.org/10.1016/j.applanim.2019.104879.

Held, S.D., Špinka, M., 2011. Animal play and animal welfare. Anim. Behav. 81 (5), 891–899. https://doi.org/10.1016/j.anbehav.2011.01.007.

Helt, M.S., Eigsti, I.M., Snyder, P.J., Fein, D.A., 2010. Contagious yawning in autistic and typical development. Child Dev. 81 (5), 1620–1631. https://doi.org/10.1111/j.1467-8624.2010.01495.x.

Hess, U., Fischer, A., 2013. Emotional mimicry as social regulation. Personal. Soc. Psychol. Rev. 17, 142–157. https://doi.org/10.1177/1088868312472607.

Hoogenhout, M., van der Straaten, K., Pileggi, L.A., Malcolm-Smith, S., 2013. Young children display contagious yawning when looking at the eyes. J. Child Adolesc. Behav. 1 (2) https://doi.org/10.4172/jcalb.1000101.

Hoppitt, W., Laland, K., 2008. Chapter 3 Social Processes Influencing Learning in Animals: A Review of the Evidence. Adv. Study Behav. https://doi.org/10.1016/S0065-3454(08)00003-X.

Huber, L., Range, F., Voelkl, B., Szucsich, A., Viranyi, Z., Miklosi, A., 2009. The evolution of imitation: what do the capacities of non-human animals tell us about the mechanisms of imitation? Philos. Trans. R. Soc. B: Biol. Sci. 364 (1528), 2299–2309. https://doi.org/10.1098/rstb.2009.0060.

Iacoboni, M., 2009. Imitation, empathy, and mirror neurons. :653-70 Annu Rev. Psychol. 60. https://doi.org/10.1146/annurev.psych.60.110707.163604.

Laméris, D.W., Van Berlo, E., Sterck, E.H.M., 2020. Low relationship quality predicts scratch contagion during tense situations in orangutans (Pongo pygmaeus). Am. J. Primatol. vol. 82 (7), e23138 https://doi.org/10.1002/ajp.23138.

Langbauer Jr, W.R., 2000. Elephant communication. Zoo. Biol.: Publ. Affil. Am. Zoo. Aquar. Assoc. 19 (5), 425–445. https://doi.org/10.1002/1098-2361(2000)19:5<425::AID-ZOO11>3.0.CO;2-A.

Lee, P.C., 1987. Allomothering among African elephants. Anim. Behav. 35 (1), 278–291. https://doi.org/10.1016/S0003-3472(87)80234-8.

Lee, P.C., Moss, C.J., 2014. African elephant play, competence and social complexity. Anim. Behav. Cogn. vol. 1 (2), 144–156. https://doi.org/10.12966/abc.05.05.2014.

Lefeuvre, M., Gouat, P., Mulot, B., Cornette, R., Pouydebat, E., 2020. Behavioural variability among captive African elephants in the use of the trunk while feeding. PeerJ 8, e9678. https://doi.org/10.7717/peerj.9678.

Leighton, J., Bird, G., Orsini, C., Heyes, C., 2010. Social attitudes modulate automatic imitation. J. Exp. Soc. Psychol. 46 (6), 905–910. https://doi.org/10.1016/j.jesp.2010.07.001.

Leiva, D., De Vries, H., 2011. Steepness: testing steepness of dominance hierarchies. R package v0, 2. ⟨http://CRAN.R-project.org/package=steepness⟩.

Madsen, E.A., Persson, T., 2013. Contagious yawning in domestic dog puppies (Canis lupus familiaris): The effect of ontogeny and emotional closeness on low-level

imitation in dogs. Anim. Cogn. 16 (2), 233–240. https://doi.org/10.1007/s1007 1-012-0568-9.

Massen, J.J.M., Vermunt, D.A., Sterck, E.H.M., 2012. Male yawning is more contagious than female yawning among chimpanzees (Pan troglodytes). PLoS One vol. 7 (7), e40697. https://doi.org/10.1371/journal.pone.0040697.

McHugh, M.L., 2012. Interrater reliability: The kappa statistic. Biochem. Med. 22 (3), 276–282. https://doi.org/10.11613/BM.2012.031.

Mundry, R., Fischer, J., 1998. Use of statistical programs for nonparametric tests of small samples often leads to incorrect Pvalues: examples from animal behaviour. Anim. Behav. 56 (1), 256–259. https://doi.org/10.1006/anbe.1998.0756.

Norscia, I., Hecker, M., Caselli, M., Collarini, E., Gallego Aldama, B., Borragán Santos, S., Cordoni, G., 2024. Social play in african savannah elephants may inform selection against aggression. Curr Zool 009. https://doi.org/10.1093/cz/zoae009.

Norscia, I., Palagi, E., 2011. Yawn contagion and empathy in Homo sapiens. PloS One 6 (12), e28472. https://doi.org/10.1371/journal.pone.0028472.

Norscia, I., Zanlini, A., Gamba, M., Palagi, E., 2020. Auditory contagious yawning is highest between friends and family members: Support to the emotional bias hypothesis. Front. Psychol. vol. 11, 442. https://doi.org/10.3389/fpsyg.2020.00442.

Norscia, I., Agostini, L., Moroni, A., Caselli, M., Micheletti-Cremasco, M., Vardé, C., Palagi, E., 2021a. Yawning is more contagious in pregnant than nulliparous women: Naturalistic and experimental evidence. Hum. Nat. vol. 32, 301–325. https://doi.org/10.1007/s12110-021-09404-w.

Norscia, I., Coco, E., Robino, C., Chiero, E., Cordoni, G., 2021b. Yawn contagion in domestic pigs (Sus scrofa). Sci. Rep. 11, 1851. https://doi.org/10.1038/s41598-020-80545-1.

Norscia, I., Caselli, M., De Meo, G., Cordoni, G., Guéry, J.P., Demuru, E., 2022. Yawn contagion in bonobos: Another group, another story. Am. J. Primatol. vol. 84 (3), e23366 https://doi.org/10.1002/ajp.23366.

Ostner, J., Wilken, J., Schülke, O., 2021. Social contagion of affiliation in female macaques. R. Soc. Open Sci. 8 (1), 201538 https://doi.org/10.1098/rsos.201538.

Osvath, M. & Sima, M. Sub-adult ravens synchronize their play: a case of emotional contagion?. Anim. Behav. Cognit. 1, 197–205. https://doi.org/10.12966/abc.05.09.2014.

Palagi, E., Cordoni, G., Borgognini Tarli, S.M., 2004. Immediate and delayed benefits of play behaviour: new evidence from chimpanzees (Pan troglodytes). Ethology 110 (12), 949–962. https://doi.org/10.1111/j.1439-0310.2004.01035.x.

Palagi, E., Nicotra, V., Cordoni, G., 2015. Rapid mimicry and emotional contagion in domestic dogs. R. Soc. Open Sci. vol. 2 (12), 150505 https://doi.org/10.1098/rsos.150505.

Palagi, E., Celeghin, A., Tamietto, M., Winkielman, P., Norscia, I., 2020. The neuroethology of spontaneous mimicry and emotional contagion in human and non-human animals. Neurosci. Biobehav Rev. https://doi.org/10.1016/j.neubiorev.2020.01.020.

Panksepp, J., Panksepp, J.B., 2013. Toward a cross-species understanding of empathy, 2013 Aug Trends Neurosci. 36 (8), 489–496. https://doi.org/10.1016/j.tins.2013.04.009.

Paukner, A., Suomi, S.J., Visalberghi, E., Ferrari, P.F., 2009. Capuchin Monkeys Display Affiliation Toward Humans Who Imitate Them. Science 325 (2009), 880–883. https://doi.org/10.1126/science.1176269.

Pedruzzi, L., Aychet, J., Le Vern, L., Maglier, V., Rossard, A., Lemasson, A., Palagi, E., 2022. Familiarity modulates both intra-and interspecific yawn contagion in red-capped mangabeys. Sci. Rep. vol. 12 (1), 11138. https://doi.org/10.1038/s41598-022-15395-0.

Pellis, S.M., McKenna, M.M., 1992. Intrinsic and extrinsic influences on play fighting in rats: effects of dominance, partner's playfulness, temperament and neonatal exposure to testosterone propionate. Behav. Brain Res. 50 (1-2), 135–145. https://doi.org/10.1016/S0166-4328(05)80295-5.

Pellis, S.M., Pellis, V.C., Bell, H.C., 2010. The function of play in the development of the social brain. Am. J. Play 2 (3), 278–296. SSN-1938-0399.

Pereira, M.E., Fairbanks, L.A., 2002. Juvenile primates: life history, development and behavior, with a new foreword. University of Chicago Press.

Pettigrew, J.D., Bhagwandin, A., Haagensen, M., Manger, P.R., 2010. Visual acuity and heterogeneities of retinal ganglion cell densities and the tapetum lucidum of the African elephant (Loxodonta africana), 2010 Brain Behav. Evol. 75 (4), 251–261. https://doi.org/10.1159/000314898.

Poole, J.H., Granli, P., 2011. Signals, gestures, and behavior of African elephants. Amboseli Elephants 109–124. https://doi.org/10.7208/chicago/9780226542263.003.0008.

Preston, S.D., de Waal, F.B.M., 2002. Empathy: Its ultimate and proximate bases. Feb;25 (1):1-20; discussion 20-71 Behav. Brain Sci.. https://doi.org/10.1017/s0140525x02000018.

Preston, S.D., de Waal, F.B.M., 2017. Only the PAM explains the personalized nature of empathy. , p. 769-769 Nat. Rev. Neurosci. vol. 18 (12). https://doi.org/10.1038/nrn.2017.140.

Prochazkova, E., Kret, M.E., 2017. Connecting minds and sharing emotions through mimicry: A neurocognitive model of emotional contagion. Neurosci. Biobehav. Rev. vol. 80, 99–114. https://doi.org/10.1016/j.neubiorev.2017.05.013.

Raviv, L., Jacobson, S.L., Plotnik, J.M., Bowman, J., Lynch, V., Benítez-Burraco, A., 2023. Elephants as an animal model for self-domestication. Proc. Natl. Acad. Sci. 120 (15) https://doi.org/10.1073/pnas.2208607120.

Rizzolatti, G., Fabbri-Destro, M., 2010. Mirror neurons: from discovery to autism. Exp. Brain Res. https://doi.org/10.1007/s00221-009-2002-3.

Ruhnau, B., 2000. Eigenvector-centrality—a node-centrality? Soc. Netw. 22 (4), 357–365. https://doi.org/10.1016/S0378-8733(00)00031-9.

Saqr, M., Fors, U., Nouri, J., 2018. Using social network analysis to understand online Problem-Based Learning and predict performance. PLoS ONE 13 (9), e0203590. https://doi.org/10.1371/journal.pone.0203590.

Schut, C., Grossman, S., Gieler, U., J. Kupfer, J., Yosipovitch, G., 2015. Contagious itch: what we know and what we would like to know. Front. Hum. Neurosci. https://doi.org/10.3389/fnhum.2015.00057.

Schütz-Bosbach, S., Prinz, W., 2015. Mirrors match minds. In: Ferrari, P.F., Rizzolatti, G. (Eds.), New frontiers in mirror neurons research. Oxford University Press, pp. 198–221. https://doi.org/10.1093/acprof:oso/9780199686155.003.0011.

Schwing, R., Nelson, X.J., Wein, A., Parsons, S., 2017. Positive emotional contagion in a New Zealand parrot. Curr. Biol. 27 (6), R213–R214. https://doi.org/10.1016/j.cub.2017.02.020.

Siegel, S., Castellan, N.J., 1988. Nonparametric Statistics for the Behavioural Sciences, 2nd edition. McGraw-Hill Book Company, New York. ISBN 978-007057357.

Simpson, E.A., Murray, L., Paukner, A., Ferrari, P.F., 2014. The mirror neuron system as revealed through neonatal imitation: presence from birth, predictive power and evidence of plasticity. Philos. Trans. R. Soc. B: Biol. Sci. 369 (1644), 20130289. https://doi.org/10.1098/rstb.2013.0289.

Siviy, S.M., 2016. A brain motivated to play: insights into the neurobiology of playfulness. Behaviour 153 (6-7), 819–844.

Siviy, S.M., Deron, L.M., Kasten, C.R., 2011. Serotonin, motivation, and playfulness in the juvenile rat. Dev. Cogn. Neurosci. 1 (4), 606–616.

Spinka, M., Newberry, R.C., Bekoff, M., 2001. Mammalian play: training for the unexpected. Q. Rev. Biol. 76 (2), 141–168.

Špinka, M., 2012. Social dimension of emotions and its implication for animal welfare. Appl. Anim. Behav. Sci. 138 (3-4), 170–181. https://doi.org/10.1016/j.applanim.2012.02.005.

Tan, J., Hare, B., 2017. Prosociality among non-kin in bonobos and chimpanzees compared. 140–154. https://doi.org/10.1093/oso/9780198728511.003.0010.

Valdivieso-Cortadella, S., Bernardi-Gómez, C., Aureli, F., Llorente, M., Amici, F., 2023. Behavioural contagion in wild spider monkeys (Ateles geoffroyi). Res. Sq. https://doi.org/10.21203/rs.3.rs-2557586/v1.

Van Berlo, E., Díaz-Loyo, A.P., Juárez-Mora, O.E., Kret, M.E., Massen, J.J., 2020. Experimental evidence for yawn contagion in orangutans (Pongo pygmaeus). Sci. Rep. 10 (1), 22251 https://doi.org/10.1038/s41598-020-79160-x.

Varlinskaya, E.I., Spear, L.P., Spear, N.E., 1999. Social behavior and social motivation in adolescent rats: role of housing conditions and partner's activity. Physiol. Behav. 67 (4), 475–482. https://doi.org/10.1016/S0031-9384(98)00285-6.

Veenema, H.C., Das, M., Aureli, F., 1994. Methodological improvements for the study of reconciliation. Behav. Process. 31 (1), 29–37. https://doi.org/10.1016/0376-6357(94)90035-3.

Videan, E.N., Fritz, J., Schwandt, M., Howell, S., 2005. Neighbor effect: evidence of affiliative and agonistic social contagion in captive chimpanzees (Pan troglodytes). Am. J. Primatol. 66 (2), 131–144. https://doi.org/10.1002/ajp.20133.

De Vittoris, S., Caselli, M., Demuru, E., Gillespie, L., Norscia, I., 2024. Beware! Different methods lead to divergent results on yawn contagion modulation in bonobos. Am. J. Primatol. e23671. https://doi.org/10.1002/ajp.23671.

de Vries, H., Stevens, J.M.G., Vervaecke, H., 2006. Measuring and testing steepness of dominance hierarchies. Anim. Behav. 71, 585–592. https://doi.org/10.1016/j.anbehav.2005.05.015.

de Waal, F.B., Yoshihara, D., 1983. Reconciliation and redirected affection in rhesus monkeys. Behaviour 224–241. ⟨http://www.jstor.org/stable/4534264⟩.

de Waal, F.B.M., Preston, S.D., 2017. Mammalian empathy: behavioural manifestations and neural basis. Nat. Rev. Neurosci. https://doi.org/10.1038/nrn.2017.72.

Watson, C.F.I., Caldwell, C.A., 2010. Neighbor effects in marmosets: social contagion of agonism and affiliation in captive Callithrix jacchus. Am. J. Primatol. https://doi.org/10.1002/ajp.20805.

Webber, C.E., Lee, P.C., 2020. Play in elephants: wellbeing, welfare or distraction? Animals 10 (2), 305. https://doi.org/10.3390/ani10020305.

Wenig, K., Boucherie, P.H., Bugnyar, T., 2021. Early evidence for emotional play contagion in juvenile ravens. Anim. Cogn. https://doi.org/10.1007/s10071-020-01466-0.

Wheeler, L., 1966. Toward a theory of behavioral contagion. Psychol. Rev. 73 (2), 179–192. https://doi.org/10.1037/h0023023.

Wilson, M.L., Bashaw, M.J., Fountain, K., Kieschnick, S., Maple, T.L., 2006. Nocturnal behavior in a group of female African elephants (Published in affiliation with the American Zoo and Aquarium Association). Zoo. Biol. 25 (3), 173–186. https://doi.org/10.1002/zoo.20084.

Wittemyer, G., Getz, W.M., 2007. Hierarchical dominance structure and social organization in African elephants, Loxodonta africana. Anim. Behav. 73 (4), 671–681. https://doi.org/10.1016/j.anbehav.2006.10.008.

Wittemyer, G., Douglas-Hamilton, I., Getz, W.M., 2005. The socioecology of elephants: analysis of the processes creating multitiered social structures. Anim. Behav. vol. 69 (6), 1357–1371. https://doi.org/10.1016/j.anbehav.2004.08.018.

Wright, K.R., Mayhew, J.A., Sheeran, L.K., Funkhouser, J.A., Wagner, R.S., Sun, L.X., Li, J.H., 2018. Playing it cool: Characterizing social play, bout termination, and candidate play signals of juvenile and infant Tibetan macaques (Macaca thibetana). Zool. Res. 39 (4), 272.

Yu, Y., Barry, D.M., Hao, Y., Liu, X., 2017. Molecular and neural basis of contagious itch behavior in mice. Science vol. 355 (6329), 1072–1076. https://doi.org/10.1126/science.aak9748.

Zentall, T.R., 2003. Imitation by Animals: How Do They Do It? Curr. Dir. Psychol. Sci. 12 (3), 91–95. https://doi.org/10.1111/1467-8721.01237.

Zentall, T.R., 2012. Perspectives on observational learning in animals. J. Comp. Psychol. 126 (2), 114–128. https://doi.org/10.1037/a0025381.