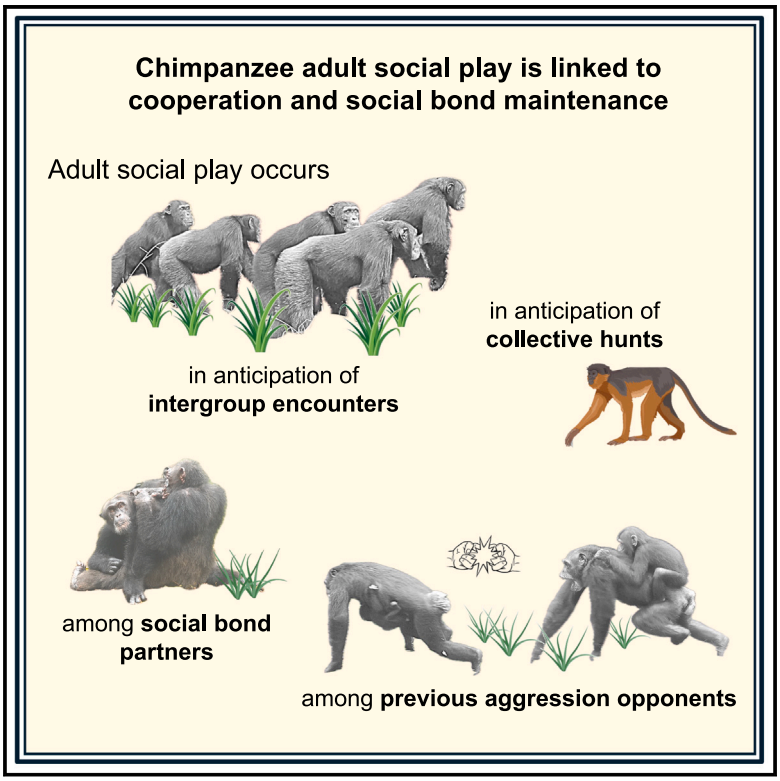
Report

Current Biology

Social play fosters cooperation in wild adult chimpanzees

Graphical abstract



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In brief

Samuni et al. show that adult chimpanzee social play serves a range of functions, from diffusing tension to supporting social bonds and collective cooperation. Their study demonstrates the sustained significance of play throughout the chimpanzee lifespan, highlighting that the social benefits derived from play outweigh its energetic costs.

Highlights

- Social play occurs throughout the chimpanzee lifespan, serving various functions
- Chimpanzee social play precedes and promotes collective cooperation
- Adult chimpanzees play more in tense situations and following intragroup conflicts
- Social familiarity influences adult chimpanzee selection of play partners

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Report

Social play fosters cooperation in wild adult chimpanzees

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SUMMARY

Adult social play is a universal human trait, promoting the tolerance, bonding, cooperation, and collective action that sustain our large and complex societies.[1,2] Play serves as a conduit for transmitting positive emotions, thereby stimulating psychological resilience to stressors and facilitating the positive intent and trust[3–6] essential for cooperation emergence. In contrast, non-human adult social play is considered rare, and its role in cooperation remains unknown. We address this gap by studying the play behavior of 57 adult chimpanzees (*Pan troglodytes*) in Taï National Park, Côte d'Ivoire, where adult social play and collective action regularly occur. We show that adult female and male chimpanzees play more during times of increased mate competition (with males mainly playing with immatures) and with adult partners they had recent disputes with, highlighting the role of play in regulating social tension that can undermine cooperation. Chimpanzees also preferred playing with adult partners with whom they share strong affiliative bonds, aligning with the idea that play is associated with social familiarity and trust. Finally, adult chimpanzees were more likely to play before collectively defending their territory against outsiders and hunting monkeys. Those who played together were subsequently more likely to collaborate, reinforcing the notion that the positive feedback signaled via play can facilitate cooperation.[5] Our findings demonstrate the sustained significance of adult social play throughout the chimpanzee lifespan, providing valuable insights into the evolution of adult social play and its societal functions, from diffusing tension to supporting social bonds and collective action.

RESULTS

We studied the social play behavior of 57 adults (>12 years) from three wild chimpanzee communities in the Taï National Park, Côte d'Ivoire. Over a 6-year study period, we documented a total of 4,966 play sessions with 6,812 play interactions involving at least one adult individual ($n_{adult\text{-}infant}$ = 4,322, $n_{adult\text{-}juvenile}$ = 762, $n_{adult\text{-}adolescent}$ = 799, $n_{adult\text{-}adult}$ = 929; Table S1; see STAR Methods for definitions). Social play occurs throughout the chimpanzee lifespan (Figure S1), underscoring that its evolutionary functions extend beyond its role in the cognitive, social, and motor development of immature individuals.[7,8]

The social play of adult chimpanzees in Taï encompassed a wide range of play types, such as wrestling, tickling, chasing, swinging, pulling, and mock biting[9] (Video S1). Although less common, adult social play also incorporated objects and substrates such as logs, fruits, snail shells, sand, and water. Play behavior was not always dyadic, and 18% of play sessions (887/4,966) involved more than one partner (i.e., polyadic play), with the largest adult play session including five individuals simultaneously playing together. One of these polyadic play sessions involved four adult males and an orphan infant male from the East community playing as the community was initiating a territorial border patrol.

The conditions underlying adult chimpanzee social play

To date, research into the drivers and functions of adult social play, primarily conducted in captive settings, has demonstrated its role in regulating social tension,[10,11] facilitating social assessment,[12–16] and promoting tolerance and bonding.[16–20] However, our understanding of how adult social play reinforces coordination and collective cooperation remains limited, partly due to the inherent constraints on cooperation in captive settings. The regular occurrence of adult social play and collective cooperation in Taï offers an avenue to examine the evolutionary significance of play and its broad social functions. Specifically, the mutualistic and synchronized nature of social play, the positive physical contact it involves, and its potential anxiolytic effects may serve to support cooperation.

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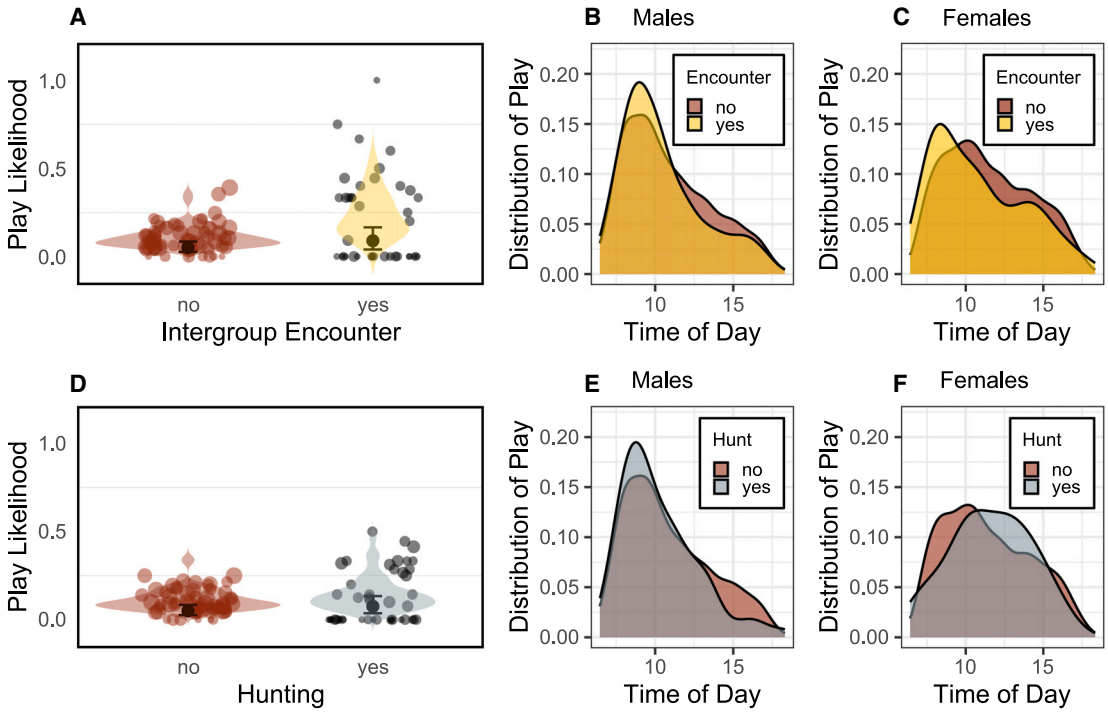

Figure 1. Chimpanzee adult-adult social play and cooperation

(A–F) Adult male and female chimpanzees are more likely to play with other adults on days in which (A) they participated in intergroup encounters (estimate = 0.56, $CI_{89\%}$ = 0.16–0.97) and (B) hunting (estimate = 0.46, $CI_{89\%}$ = 0.14–0.78), with most adult-adult play interactions occurring before the initiation of the collective territorial act (80%) or hunting (79%). Shown are the posterior means (circles), 95% credible intervals (error bars), predicted individual probabilities from the posterior distribution of the model (violin), and individual play probabilities from the raw data (dots), with the size denoting the number of observations. Evaluating the distributions of play interaction probabilities throughout the day demonstrates a stronger peak of adult play on days of intergroup encounters (B) and hunting (E) in males and an earlier peak of adult play on days of intergroup encounters (C), but not hunting (F), in females, compared with days without these events. See Table S2 for descriptive statistics and Figure S2 for similar results using adult social play with partners of all ages.

Social play could impact cooperation in various ways. Play may facilitate engagement in cooperative acts or support cooperation by mitigating factors that could undermine it, like social tension. We examined the conditions impacting the occurrence of play in adult chimpanzees, both for play with other adults and play with partners of all ages, as their links to cooperation may differ. For example, because other adults are the typical partners in collective cooperation, adult-adult play may be more beneficial in these contexts than play between adults and immatures. We found strong links between play and cooperation (Table S2). Social play of adult male and female chimpanzees with other adults was 75% more likely to occur on days in which these individuals also collectively defended their territory against out-groups (estimate = 0.56, confidence interval $[CI]_{89\%}$ = 0.16–0.97, Figure 1) and 58% more likely to occur on days when individuals jointly hunted monkeys (estimate = 0.46, $CI_{89\%}$ = 0.14–0.78, Figure 1). These effects remained largely consistent when examining play behavior of adults with partners of all ages, the only difference being that males, but not females, played more on hunting days (estimate = 0.52, $CI_{89\%}$ = 0.07–1.02, Figure S2; Table S2).

We also found that adult female chimpanzees, but not adult males, were 46% more likely to play with other adults on days when at least one of the females in the group showed maximal tumescence (Table S2), a context known to trigger within-group aggression and tension.[21,22] In contrast, when focusing on social play of adults with partners of all ages, we found that both sexes were 32% more likely to play (estimate = 0.27, $CI_{89\%}$ = 0.13–0.41, Figure 2) in the presence of maximally tumescent females. These differences suggest that on such days, social play may serve different functions for males and females. For example, while female social play on these days is likely associated with tension reduction, adult males competing for mating opportunities might engage in play with immatures as a form of a mating strategy.

Individuals' ecological and social environments also influenced adult play likelihood. A one-standard-deviation increase in ripe fruit availability (Figures 2 and S3) or average party size increased play odds by a factor of 1.45 and 1.48, respectively (Table S2; similar patterns found for play with partners of all ages). Finally, dominance rank had no clear effect on adult play likelihood, but social play with adult partners showed a decline with increasing age (estimate = −0.35, $CI_{89\%}$ = −0.60 – −0.10).

Chimpanzees play in anticipation of collective cooperation

To disentangle the role of play in cooperation reinforcement versus tension regulation, we further examined whether the observed increase of adult social play preceded or occurred after intergroup encounters and hunts. Overall, most adult play

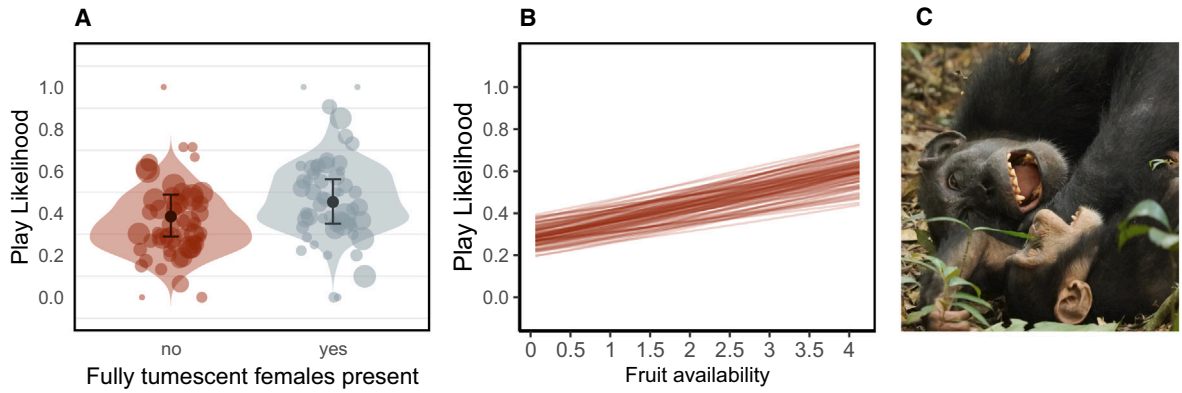

Figure 2. Social and ecological correlates of adult chimpanzee social play

Adult male and female chimpanzees are more likely to play socially with individuals of all ages when (A and B) (A) fully tumescent females are present (estimate = 0.27, $CI_{89\%}$ = 0.13–0.41) and (B) at times of high food availability (estimate = 0.32, $CI_{89\%}$ = 0.24–0.40). Shown are (A) the posterior means (circles), 95% credible intervals (error bars), predicted individual probabilities from the posterior distribution of the model (violin), individual play probabilities from the raw data (dots), with the size denoting the number of observations, and (B) the posterior draws (lines).

(C) Social play between an adult female chimpanzee and an unrelated female juvenile, © Liran Samuni, Taï Chimpanzee Project. See Table S2 for descriptive statistics.

interactions occurred before (before intergroup encounter: 80%, before hunt: 79%), rather than after, the start of the collective act (mean start times—encounter: 11:35 am ± 2.8 h, hunt: 12:15 pm ± 2.6 h). However, because adult social play was generally more likely to occur before midday (Figure S3; play with partners of all ages—62%, adult-adult play 69%), we needed to determine whether this increased play likelihood before intergroup encounters and hunts was due to the time of day or the collective act itself. Using data permutations (see supplemental information), we found that the increased likelihood of adult-adult play before the collective activities was significantly higher than expected based solely on timing (encounter: *observed* play proportion = 0.75; mean *expected* proportion = 0.45 ± 0.027; $p < 0.001$; hunt: *observed* play proportion = 0.80; *expected* = 0.43 ± 0.023; $p < 0.001$; Figure S4), suggesting that chimpanzees play in anticipation of collective cooperation.

A visual inspection of the distribution of social play interactions throughout the day (Figures 1 and S2) largely confirms these patterns, demonstrating that intergroup encounters (for males and females) and hunting (for males only) are both associated with a distinct early peak in social play that differs from days in which neither an encounter nor a hunt occurred.

Social play promotes participation in collective cooperation

Chimpanzee territorial defense and hunting both rely on a coordinated group effort, where the benefits are more likely to be achieved through collective engagement,[23–27] making it harder to regulate than dyadic cooperation.

The positive emotions and coordination associated with play[3–6] may function as signals of cooperative motivation and facilitate collaboration. To evaluate whether social play promotes cooperation, we examined whether adult partners who played together were subsequently more likely to collaborate in territorial defense and hunting compared to times when they had the opportunity to play but did not. We found that the same partners were 5 times more likely to participate in intergroup encounters (estimate = 1.67, $CI_{89\%}$ = 0.34–3.11) and 2.6 times more likely to engage in hunts (estimate = 0.98, $CI_{89\%}$ = 0.15–1.79) if they played together beforehand. On average, these play interactions occurred over 3 h before the collective activities (encounter: 3.25 ± 2 h; hunt: 3.5 ± 2 h), suggesting that their co-occurrence is not merely due to temporal proximity. In Taï, intergroup encounters and hunts are frequently preceded by coordinated, goal-oriented movements that serve to scout territorial borders or search for monkeys.[25,26] The occurrence of these patrols emphasizes the anticipation involved in these activities. Additionally, we observed that polyadic play among adults occurred twice as often on days of intergroup conflicts (28% of play interactions) and was slightly more frequent on hunting days (18%) compared with days without these activities (14%). It remains to be tested whether adult play interactions are qualitatively different when occurring in the context of collective cooperation relative to other situations, for example, by incorporating more panting vocalizations.

The social environment and play partner selection

To further evaluate the link between social play and cooperation, bonding, and tension regulation, we tested chimpanzee play partner decisions (which other adult individuals chimpanzees choose to play with). The predictor best explaining play partner selection was whether an aggression occurred between partners in the previous 30 min (estimate = 1.31, $CI_{89\%}$ = 1.02–1.61; Figure 3; Table S3), which increased play likelihood between these partners by 271%. Further, play likelihood was higher the stronger the grooming relationship was between individuals, with an increase of one-standard-deviation in the grooming score increasing play likelihood by 42% (estimate = 0.35, $CI_{89\%}$ = 0.23–0.48; Figure 3). Adults of all ages were more likely to play with younger adults (odds ratio = 0.73), and social play was less likely when both the focal and partner were low-ranking individuals (odds ratio = 1.22). Finally, adult females were more likely to select adult males as play partners whereas males were as likely to select males and females (Table S3).

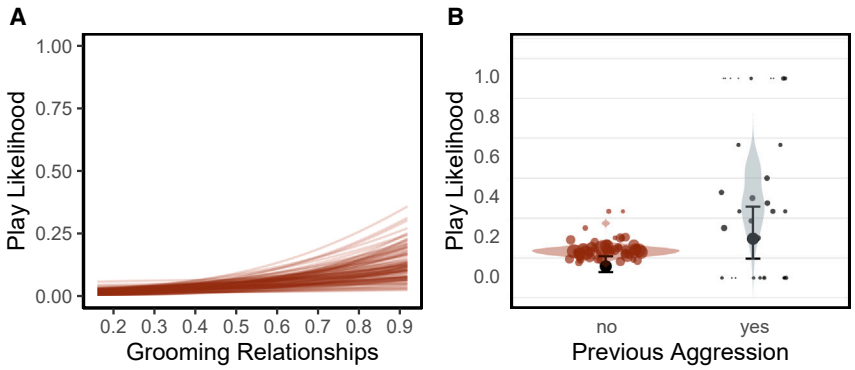

Figure 3. Social play partner selection in chimpanzees

Adult male and female chimpanzees are more likely to (A) choose play partners with whom they maintain stronger grooming relationships (estimate = 0.35, $CI_{89\%}$ = 0.23–0.48) or (B) choose previous aggression opponents (<30 min; estimate = 1.31, $CI_{89\%}$ = 1.02–1.61) as play partners. Shown are (A) the posterior draws (lines) or (B) the posterior means (circles), 95% credible intervals (error bars), predicted individual probabilities from the posterior distribution of the model (violin), individual play probabilities from the raw data (dots), with the size denoting the number of observations. See Table S3 for descriptive statistics.

DISCUSSION

The interplay between ecological, social, and individual factors influences when and with whom social play behavior of adult chimpanzees takes place. In line with the idea of energetic constraints on adult chimpanzee play behavior,[28] we showed that ripe fruit availability and seasonality both had a strong influence on adult chimpanzee play occurrence. Evaluating the social factors underlying adult play, we show that play behavior of females and males (with immatures) increases in tense situations, such as during times of enhanced mate competition. Social play was also more likely among adult partners who had recently engaged in aggression and those with stronger grooming relationships. Lastly, both male and female chimpanzees played, particularly with other adults, in anticipation of intergroup encounters and hunts and were more likely to collaborate in these activities with those they played with. These patterns occurred independently of variation in the ecology, strengthening the idea that the social benefits derived from play outweigh its immediate energetic costs.

Living in social groups has its benefits and costs, and group members must regularly navigate their social interactions across different scales and contexts to secure a positive net gain. For example, the individuals one competes with today for food or mates are often tomorrow's cooperation partners when a joint goal is shared. Our results suggest that social play offers chimpanzees a pathway to preserve social connectivity within groups. In line with the hypotheses that play serves to regulate social tension,[10,11] we show that chimpanzee play may facilitate reconciliation after conflicts[29] and alleviate some consequences of within-group competition. The positive properties of social play behavior are modulated by brain reward circuits,[6,30] which can act to reduce stress and enhance emotional well-being. Chimpanzee play is also often accompanied by a play face and panting vocalizations akin to human smiles and laughter, which can additionally serve to convey positive emotions, reduce anxiety, and promote coordination.[31]

Social tension can also explain why male and female chimpanzees are more likely to play on days in which they engaged in intergroup conflict and hunts. Chimpanzee intergroup conflict is highly risky due to the violent and unpredictable nature of these interactions.[32–34] Across populations, including Taï, intergroup encounters are associated with increased cortisol secretion,[22,35,36] highlighting the tense nature of these competitive acts. Similarly, although hunting is not known to impact cortisol secretion in our study population[22] (but cf. Sobolewski[36]), the resulting meat consumption induces competition.[37] Therefore, the heightened play likelihood observed on these days may initially appear to be purely a product of increased tension. Challenging this notion, however, is the finding that the majority of all play interactions during these days occurred before the onset of collective acts, a pattern that could not be attributed solely to the timing of these events. Showing that adult chimpanzees are more likely to play on days of intergroup encounters and hunts—doing so before initiating the risky collective acts—and that those who played were more likely to subsequently collaborate, reinforces the idea that social play can serve as a pathway to support bonding and coordination.[2,17] Here, play may act in a similar way to anticipatory grooming,[33] potentially signaling cooperative motivation, and may offer a valuable context for examining the existence and nature of planning in wild animals. It is important to note that tension reduction and cooperation reinforcement are not mutually exclusive and that it is the interplay of the two that is likely to be the most efficient in supporting cooperation.

Social play behavior requires individuals to communicate, synchronize actions, and respond to one another's behaviors, closely resembling the coordination seen in joint action scenarios.[5,38] The involvement of intense physical contact during play, which often resembles the actions occurring in aggressive interactions (e.g., slapping, biting, chasing, and jumping on), likely builds on or reinforces trust between partners. As such, the joint engagement coupled with the physical intensity of the act potentially allows for providing feedback of partners' willingness to cooperate and thus may reduce social uncertainty and improve signaling efficiency around these interactions. Here, the joint understanding of the playful intent and the simultaneous engagement of partners makes play particularly beneficial in promoting subsequent coordination between partners,[5] like in the case of collective action during intergroup encounters and hunts. Although we have found that adult social play preludes collective cooperation, it remains to be tested whether this link involves strategic decision making by chimpanzees or is driven by emotional or motivational processes.

In human societies, social play is proposed to promote cooperation by mitigating aggression,[39] with more tolerant and cooperative hunter-gatherer societies exhibiting higher rates of adult social play.[2] This notion extends to non-human primates and social carnivores, where societies marked by tolerance and cooperation are likewise argued to exhibit a greater likelihood to

engage in adult play.[17] The considerable diversity in tolerance and cooperation observed across chimpanzee populations[40] offers an excellent opportunity to leverage this variation and directly test this theory within a single species. We expect that the Taï chimpanzees, known for increased group cohesion and the regular participation of both sexes in collective cooperation,[25,40,41] would exhibit elevated rates of adult play compared to less cohesive chimpanzee populations.

The high frequency of adult social play in our study (41% of n = 4,318 observation days) challenges the idea that play in adult chimpanzees is rare[42] and permits examinations into understudied aspects of adult behavior in the wild. Our finding that adult social play occurs in association with collective cooperation, such as hunting and intergroup encounters, resonates with observations in canids, where social play is thought to facilitate hunting activities.[20,43] Similarly, in humans, games, dances, and rituals are thought to stabilize collective action in the contexts of warfare and hunting by fostering joint commitment and bonding.[44–46] While social play may be less formalized and structured than games or rituals,[47] it shares key features that are likely effective in promoting bonding, cooperation, and collective decisions of highly social species.

RESOURCE AVAILABILITY

Lead contact

Any requests for further information and resources should be directed to and will be fulfilled by the lead contact, Liran Samuni (liransamuni@gmail.com).

Materials availability

This study did not generate new unique materials, e.g., reagents.

Data and code availability

- The data used in this study have been deposited at GitHub and are publicly available for download at https://doi.org/10.5281/zenodo.14101619 and in the key resources table.
- The R code for statistical tests has been deposited at GitHub and is publicly available at https://doi.org/10.5281/zenodo.14101619.
- Any additional information required to reanalyze the data reported in this paper is available from the lead contact upon request.

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AUTHOR CONTRIBUTIONS

L.S., A.M., C.C., and R.M.W. conceptualized the study. L.S. and A.M. collected the data and designed the methodology. L.S. conducted the formal analysis and drafted the paper. L.S., A.M., C.C., and R.M.W. reviewed and edited the paper.

DECLARATION OF INTERESTS

The authors declare no competing interests.

STAR★METHODS

Detailed methods are provided in the online version of this paper and include the following:

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SUPPLEMENTAL INFORMATION

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STAR★METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Deposited data		
Data	https://doi.org/10.5281/zenodo.14101619	N/A
R Code	https://doi.org/10.5281/zenodo.14101619	N/A
Software and algorithms		
R version 4.4.0	https://www.r-project.org	N/A

EXPERIMENTAL MODEL AND SUBJECT DETAILS

We conducted our study on all adult (≥ 12 yrs, *N* = 57 individuals) male and female chimpanzees (*Pan troglodytes verus*) of three communities (i.e., North, South and East, Table S4) at the Taï National Park, Côte d'Ivoire (5°45'N, 7°07'W),[48] between January 2012- January 2018. We define adulthood as beginning at age 12 because, by this age, chimpanzees in Taï are fully integrated into the dominance hierarchy and range independently. Specifically, two males in this study became alpha males by ages 12 and 14, despite having several older competitors in their prime.

We collected our data during full-day focal follows[49] (*n* = 4318 days). We documented all changes in activity, social interactions (e.g., grooming, play, aggression), and vocalizations involving the focal individual.[50] Due to the fission-fusion social dynamics of chimpanzee groups,[41,42] we continuously recorded changes in the size and composition of association parties, allowing us to capture the availability of play partners. In addition to focal follow data collection, we recorded *ad-libitum* the occurrence of all hunting and intergroup encounters, including the start of the event and the identity of participants. Finally, we also collected daily data on the reproductive status of females, noting whether females showed maximal tumescence.

All methods used in this study were non-invasive and were approved by the Ministries of Research and Environment of Côte d'Ivoire, and Office Ivoirien des Parcs et Réserves. All aspects of the study comply with the ethics policy of the American Society of Primatologists.

METHOD DETAILS

Adult social play

Chimpanzee social play incorporates a complex combination of actions and signals, turn-taking of play roles, the use of objects during play, and gestural and vocal signaling of play intent and invitation.[9,51–54] Chimpanzee play can involve more than two partners and occurs among individuals of all ages, despite higher frequency in immature individuals.

We categorized adult social play as any play behavior that involved at least one individual aged 12 years or older. Play behaviors included swinging, wrestling, tickling, chasing, slapping, and mock biting and were often accompanied by a play face and panting vocalizations (Video S1). We categorized play into sessions and interactions: a play session refers to the consecutive play activity of the focal individual irrespective of the partner identity (i.e., the focal is playing), while a play interaction pertains to play activity with a specific partner (i.e., the focal is playing with A). As such, a play session can include multiple play interactions. As chimpanzee social play often includes short breaks, we categorized play behaviors as a single session or interaction if they occurred within one-minute of each another. We provide the distribution of adult social play interactions across age classes in the supplementary materials (Figure S1; Table S1). Across our dataset, adult females had higher tendencies to play with infants relative to males, whereas males tended to play more often with non-infant partners relative to females (Table S1). The longest adult-adult play interaction observed was 20min in duration, whereas the longest adult-infant, adult-juvenile, and adult-adolescent play interactions were ~30min in duration each.

Social relationship strength and dominance rank

To characterize the strength of the grooming relationships of individuals, we implemented the Dynamic Dyadic Sociality Index.[55–57] This method provides continuous daily measures for grooming strength for each combination of adult individuals within each group. To evaluate the grooming strength, we relied on grooming interactions collected during focal follows between 2011–2018 (grooming bouts: East – 9,533, North – 8,207, South – 13,191). Using grooming data starting in 2011 we could account for a necessary burn-in phase of the method, which ensures that a sufficient number of grooming interactions are included before the index is considered reliable and representative. The higher the DDSI values the more grooming partners invested in one another.

To assess within-group dominance relationships in the three communities we applied a likelihood-based adaptation of the Elo rating approach,[56,58,59] using submissive unidirectional pant grunt vocalizations. We estimated a mixed-sex dominance hierarchy for

each community, using pant grunt data collected between 2011-2018 (pant grunt vocalizations: East – 9,548, North – 7,881, and South – 14,734). We standardized the Elo rating values to a range from 0 to 1, with 1 representing the highest ranking individual of each community.

Fruit availability

As fruit availability is known to impact adult chimpanzee play behavior,[28] we calculated a monthly ripe fruit availability index based on the absence/presence of mature fruits, and the density and mean basal area of tree species. Phenology data was collected monthly along phenology transects within the home-range of each chimpanzee community with a total of 2,623 trees monitored monthly. Thus, our metric of fruit availability reflects local variation in ripe fruit productivity which has been previously demonstrated to be a strong predictor of sugar intake.[60]

QUANTIFICATION AND STATISTICAL ANALYSIS

All models were fitted in R v4.0.4[61] using the 'brms'[62] and 'Rstan'[63] packages. Posterior estimates were generated using the Hamiltonian Monte Carlo algorithm. We used 3,000 iterations for four chains; chain convergence was assessed by visual inspection of trace plots,[64] showing no convergence problems. For all fixed effects in all models, we used weakly informative, normal priors,[65] and standardized all continuous variables to a mean of zero and a standard deviation of one.[66] We assessed Variance inflation factors (VIF) using the R package 'car'[67] which revealed no collinearity problems (all VIF < 8). We used the *bayes_R2* function to evaluate the proportion of variance explained by the fitted model (R^2).[68]

When do adult chimpanzees play?

To test when adult chimpanzees play socially, we fitted a Bayesian generalized linear model with a binomial response variable (response 0 = no play, 1 = play) and logit link function. The datapoints in this model were the focal observation days, with play occurring in 1769 (play with partners of all ages) or 539 (adult-adult play) out of 4318 of focal days (40,594 observation hours). To test our predictions, we included as fixed effects the occurrence of an intergroup encounter or a hunt and the presence of fully tumescent females and their interaction with the sex of the focal. If the 89% credible intervals of an interaction term crossed zero, we re-ran the model without the specific interaction. We also included the monthly fruit availability, seasonality (depicted as the sine and cosine of date, Figure S3), average party size during the focal observation day, and the age, dominance rank, and group identity of the focal individual. We included the log-transformed observation duration as an offset term. As random effects we added the day and focal identities and all random slopes with sufficient variation within the levels of the random effects, including the average party size within each of the identities, the age and rank within day, and food availability and seasonality within individual. Our dataset for this model included 1888 unique days (i.e., dates) and 57 focal individuals belonging to three communities. We fitted this model twice: either focusing exclusively on play behavior with adult partners or including play behavior with partners of all ages (Table S2).

Does adult-adult play promote collaborations?

To determine whether adult partners that played subsequently participated together (0 = no, 1 = yes) in intergroup encounters or hunt, we fitted two binomial Bayesian generalized linear models with a logit link function (one for intergroup encounters and one for hunting). The model datapoints represent either intergroup encounter or hunt days, indicating if the focal individual played with a partner beforehand and whether they subsequently engaged in these activities with the same partner. We included only those days when an intergroup encounter or a hunt occurred, and partners were observed together in the same party, indicating an opportunity for both play and collective cooperation. Additionally, we focused on adult-adult dyads that played together at least once, thus applying a within-dyad design. As fixed effects we used preceding play occurrence (yes/no), dyadic sex combination, and group identity, while focal, partner, dyad, and event identities were included as random effects. We included focal and partner as multi-membership random effects, indicating that each individual can belong to either grouping factors. Our dataset for the hunt model comprised 186 hunt events and 38 dyads, with partners jointly participating in 462 out of 781 opportunities. For the intergroup encounter model, we had 104 events and 44 dyads, with partners jointly participating in 361 out of 456 opportunities.

With whom do adult chimpanzee play?

To investigate play partner selection between adult chimpanzees, we implemented conditional logistic regression analysis in a Bayesian framework using the 'stan_logit' function in the 'rstanarm' package.[69] Specifically, we investigated what influenced play decisions with certain partners over others, by including all adult bystanders as potential play partners during a given play *event* and marking whether they played (1) or not (0). By including only the adults present in the focal individual's party during the event as potential play partners, this approach ensures that play selection reflects individual, social, or ecological processes rather than mere play opportunities. To capture play partner selection accurately at a given time point (i.e., I played with A and C but not with D), we analyzed the data at the level of a play *event* rather than play interactions. This approach minimizes the risk of falsely assigning '0' to partners with whom the focal individual interacted. To account for the time window necessary to capture play decisions with different partners occurring in temporal proximity, we defined *play events* as starting from the onset of a focal social play with another adult until a cessation of play for more than five minutes, noting all participating adult play partners and bystanders present in the

event. We chose a five-minute threshold for defining a play event because, in over 85% of cases, the latency between play sessions with the same availability of partners (i.e., party composition) fell within this timeframe.

Data were stratified within each play event, such that all potential play partners were compared and tested against each other. As fixed effects we included the grooming DDSI value between the focal and potential play partner (representing the strength of their social relationship) and whether an aggression occurred between the two during the 30 minutes preceding the play event. We also included the group identity and the two-way interactions between the ages, dominance ranks, and sexes of the focal and potential partners. Including the two-way interactions allowed us to evaluate both the absolute and relative impact of rank, age, or sex on play likelihood.[70] We also included random intercepts for the potential partner and dyad. Our dataset for this model included 5051 potential play decisions (no play = 4333 and play = 718) with 57 potential play partners, 415 dyads, and 655 play events. We did not account for kinship in this analysis because only 10 out of the 415 dyads were maternal kin (three dyads in South and seven in North) and these few kin dyads showed dependencies based on sex and group (i.e., no maternal brothers, no kin in East).

Data permutations

We conducted data permutations to determine whether adult social play preceding intergroup encounters or hunts occurs at higher rates compared to what would be expected based solely on the timing of these activities. This procedure enabled us to disentangle whether it is the time of day or the anticipation of collective action that drives increased play likelihood.

We calculated the *observed* play proportion by estimating the true frequency of days showing play before intergroup encounters or hunts. We then randomly assigned the observed (real-life) timings of intergroup encounters or hunts to a dataset of days lacking these collective acts. We repeated this procedure 1,000 times, while keeping the focal identity information and play interactions constant. In each randomized dataset, we evaluated the proportion of days during which play occurred before the start of intergroup encounters or hunts (*expected* proportion) and compared it with the *observed* proportion. We repeated this procedure, considering play interactions with partners of all ages and exclusively with adults (Figure S4). Given the sex-specific impact of hunting on social play occurrence, we conducted the hunting permutations with partners of all ages only using data on male focal follows. *P*-values are represented as the ratio number of permutations wherein the *expected* proportion exceeded the *observed* proportion to the total number of permutations.