Sex differences in early experience and the development of aggression in wild chimpanzees

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Edited by Christopher W. Kuzawa, Northwestern University, Evanston, IL, and approved January 27, 2021 (received for review August 12, 2020)

Sex differences in physical aggression occur across human cultures and are thought to be influenced by active sex role reinforcement. However, sex differences in aggression also exist in our close evolutionary relatives, chimpanzees, who do not engage in active teaching, but do exhibit long juvenile periods and complex social systems that allow differential experience to shape behavior. Here we ask whether early life exposure to aggression is sexually dimorphic in wild chimpanzees and, if so, whether other aspects of early sociality contribute to this difference. Using 13 y of all-occurrence aggression data collected from the Kanyawara community of chimpanzees (2005 to 2017), we determined that young male chimpanzees were victims of aggression more often than females by between 4 and 5 (i.e., early in juvenility). Combining long-term aggression data with data from a targeted study of social development (2015 to 2017), we found that two potential risk factors for aggression—time spent near adult males and time spent away from mothers—did not differ between young males and females. Instead, the major risk factor for receiving aggression was the amount of aggression that young chimpanzees displayed, which was higher for males than females throughout the juvenile period. In multivariate models, sex did not mediate this relationship, suggesting that other chimpanzees did not target young males specifically, but instead responded to individual behavior that differed by sex. Thus, social experience differed by sex even in the absence of explicit gender socialization, but experiential differences were shaped by early-emerging sex differences in behavior.

aggressive development | social development | fission–fusion | early social experience | exposure to aggression

In many animal societies aggression is integral to negotiating access to fitness-enhancing resources, such as food and mating opportunities. Sexual selection and parental investment theories predict that social strategies employed by males, including the frequency and forms of aggression, will often differ from those of females, owing to differing constraints on male and female reproduction (1). Whereas males are generally expected to use riskier, more costly forms of physical aggression in the context of mating competition, females are expected to reserve such behaviors for protecting offspring and defending resources (2). These behavioral differences emerge between birth and reproductive maturity through social and physiological processes of development that include early life social experience and social learning. In this study, we ask whether aggressive experience during development differs between male and female chimpanzees in ways that anticipate adult sex differences in aggressive behavior, and if so, how such differences develop.

Social influences on aggressive development have been studied intensively among children. Like other mammals, humans exhibit marked sex differences in physical aggression. Across cultures men are more likely than women to start physical fights (3–5), commit violent crimes (6, 7), and die violent deaths (8). Boys are more physically aggressive than girls by 2 to 3 y old, and this difference increases with age (9–11). This pattern has often been explained as the result of differences in the ways that boys and girls are socialized, including gender-specific rules surrounding the use of physical aggression (11–16). Indeed, cross-cultural studies have revealed that cultural differences in socialization processes can impact the magnitude of gender differences in physical aggression across human cultural groups (5, 12, 17–19). However, nowhere are women more physically aggressive than men, or girls more physically aggressive than boys. Although the global distribution of girls' and boys' aggressiveness may overlap, with girls in some cultures being more physically aggressive than boys in other cultures, within-population analyses consistently report that boys, on average, are more physically aggressive than girls from the same population (12, 20, 21). The occurrence of similar sex differences in physical aggression among other primates (reviewed in ref. 22), suggests that humans could have inherited this behavioral pattern from our evolutionary ancestors. Since other primates rarely if ever engage in active teaching (23, 24), this suggests that the difference is driven, at least in part, by developmental mechanisms other than direct socialization.

One well-established mechanism is neurophysiology, as evidence from a variety of species indicates that androgens exert both organizational and activational effects on male behavior that promote aggressive competition with other males (reviewed in refs. 25–30). A less well-explored possibility is that sex differences can emerge from other differences in social experience, such as through differences in social learning and differential exposure to social stimuli. In other words, sex differences may be learned without being explicitly taught. There is evidence that

Significance

Chimpanzees, human's close evolutionary relatives, are a tractable model system for understanding how physical aggression can develop in the absence of gender socialization. Here we used 13 y of behavioral data and a targeted 3-y social development study to document clear sex differences in chimpanzees' early aggressive experiences, supporting the possibility for social experience to shape sex-typed behavior in the absence of explicitly taught gender norms. However, as young males' own aggressive behavior provoked aggressive responses from others, experiential differences were influenced by early-emerging behavioral differences that already resembled adult patterns. By demonstrating interactions between exposure to aggression and developing behavior, our results add an important perspective to long-standing debates over the origins of gender differences in human aggression.

Author contributions: K.H.S., M.E.T., and M.N.M. designed research; K.H.S., M.E.T., Z.P.M., E.O., R.W.W., and M.N.M. performed research; K.H.S. and Z.P.M. analyzed data; and K.H.S., M.E.T., and M.N.M. wrote the paper.

The authors declare no competing interest.

This article is a PNAS Direct Submission.

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This article contains supporting information online at https://www.pnas.org/lookup/suppl/doi:10.1073/pnas.2017144118/-/DCSupplemental.

Published March 16, 2021.

such mechanisms play a role in children's aggressive development. For instance, from a young age, children are more likely to model the physically aggressive behavior of same-gender adults (31, 32) and self-segregate into same-gender play groups where boys play more roughly than girls (33, 34). However, the importance of these alternative mechanisms is difficult to assess in humans because socialization is pervasive and entangled with other aspects of developmental experience (10, 22). This problem is further complicated by our long childhoods and the difficulties of observing behavior longitudinally in human populations (10).

Experimental studies on animal models can isolate and investigate the impacts of specific aspects of early experience on behavioral development. Such work has underscored the importance of social exposure and observational learning to the development of physical aggression across diverse taxa (crayfish [*Procambarus clarkii*], ref. 35; black-headed gulls [*Larus ridibu*], ref. 36; and macaques [*Macaca mulatta*], ref. 37). For example, while black-headed gulls express aggressive territorial responses even when raised in isolation, they do not develop species-typical agonistic displays unless raised in groups with exposure to adult models that perform them (36). This suggests that, like other complex behaviors, components of agonistic behavior, including the details of when, how, and toward whom to direct aggression are socially learned through observation or direct interaction with older, more experienced social models (24, 36). However, most previous experimental work has either lumped both sexes together or tested only one sex and, therefore, cannot be applied to whether and how social experience and learning differ between the sexes.

Although aggressive development has rarely been explicitly studied in free-living animals, there is some evidence of sex differences in aggressive experience among primates. Subadult males of several species receive more physical aggression than females (red howler monkeys [*Alouatta seniculus*], ref. 38; macaque spp. [*Macaca*], refs. 39–41; baboon spp. [*Papio*], refs. 42, 43; Hanuman langurs [*Semnopithecus entellus*], ref. 44; but not blue monkeys [*Cercopithicus mitis*], ref. 45; or patas monkeys [*Erythrocebus patas*], ref. 46), especially around the time of puberty when they begin to exhibit status-striving behavior (reviewed in ref. 43). However, a recent developmental study of semifree ranging rhesus macaques found that males began receiving more physical aggression as early as 1 y old, long before reproductive maturity (40). Further, receiving more physical aggression was independent of differences in yearlings' behavior, leading the authors to suggest that early aggressive experience may be shaped by dispersal patterns, preparing males to leave their groups and females to remain (40).

For chimpanzees, a long developmental period and a complex social system provide ample scope for differences in experience to shape adult social behavior. Chimpanzees live in large, multimale, multifemale communities that regularly fracture into fluid subgroups or parties throughout the day (47, 48). Unlike more rigid social grouping, this "fission–fusion" system affords adults extensive flexibility and choice in their associations (49). While chimpanzees do not actively teach their offspring, immature individuals do learn socially through observation and emulation (24). Because young chimpanzees remain socially dependent upon their mothers for 8 to 10 y (48, 50), their social experiences and exposure to social learning opportunities can vary substantially based on their mothers' ranging choices and preferences (51).

Although adult chimpanzees of both sexes display acts of aggression ranging from mild threatening gestures and vocalizations to brutal, even lethal, physical attacks, males use physical aggression up to 14 times more often, and in different contexts than females (48, 52–54). Males rely on frequent dominance displays and aggressive contact with conspecifics to navigate within-group dominance hierarchies (55). They also form aggressive coalitions to defend territories and attack neighbors more often than females (55, 56). In mating contexts, male chimpanzees use aggression to increase access to fertile females (57). Although both sexes have been known to engage in infanticide, most records of attempted and successful infanticide involve adult males (58, 59). When females use aggression, they do so primarily in defense of offspring (48, 52, 60) or in direct or indirect competition over food with other females (52, 58, 61).

Here, we use long-term behavioral data from wild chimpanzees in Kibale National Park, Uganda, to test the hypothesis that immature males experience more physical aggression than similarly aged females. We used all-occurrence aggression records taken over 13 y (2005 to 2017) to determine whether males were exposed to higher rates of aggression between other group members or directly received higher rates of aggression compared to females during development.

We further hypothesized that other sex differences in early life sociality would contribute to or explain sex differences in early aggressive experience. We used focal data on chimpanzee social development (2015 to 2017) to examine four potential pathways that might increase the risk of experiencing physical aggression: spending time [P1] in parties with or [P2] in close proximity to adult males (the age-sex class that exhibits the most aggression); [P3] spatial independence from mothers (who can provide protection); and [P4] the use of aggression by the immature chimpanzee. Specifically, we predicted that [P1] immature male chimpanzees would spend more time than females associating in parties with adult males. Prior evidence for this comes from Gombe, where mothers spent more time in parties with adult males when they had infant sons versus daughters, (though this difference was limited to infants under 6 mo old) (51). We also predicted that immature male chimpanzees would spend [P2] more time in close proximity to available adult males, and/or [P3] less time in close proximity with their mothers, which may increase the risk of receiving aggression. Chimpanzee mothers tend to keep their infants in closer proximity when adult males are present, suggesting that they perceive increased risk (62, 63). Prior evidence from Gombe suggests that male chimpanzees gain earlier independence from their mothers and are more attracted to available adult male social partners (50, 64, 65). However, whether independence leads to increased receipt of aggression is unknown.

Finally, in line with previous studies of wild primates, we examined whether, [P4] even before puberty, male chimpanzees exhibit more aggressive behaviors than females. Though sex differences in the use of conventional aggression, including physical attacks and threatening behaviors, have rarely been reported among prepubertal subadults, early-emerging differences in other aspects of sociality have been reported previously at Gombe (64, 65). Thus, it is plausible that young chimpanzee males could receive more aggression from others out of retaliation for their own behavior.

After testing whether these aspects of the social environment systematically differ for young male and female chimpanzees, our final goal was to use multivariate models to directly test whether differences in one or more of these aspects of early sociality predicted individual differences in aggressive exposure.

Materials and Methods

Study Site and Population. This study includes two sets of data from the Kanyawara community of wild chimpanzees in Kibale National Park, Uganda: 1) long-term behavioral records from the Kibale Chimpanzee Project (KCP) and 2) detailed early life experience data collected by K.H.S. Originally observed by Isabirye-Basuta from 1983 to 1985 (66), the Kanyawara community has been followed continuously by KCP researchers and highly trained local field assistants since 1987 (67). During the period of data collection, all chimpanzees were individually recognized and habituated to human observers. Over the course of this study, the Kanyawara community ranged from 41 to 54 chimpanzees, including 8 to 11 adult males (15+ y old), 13 to 18 adult females (12+ y old), 9 to 17 subadult males (under 15 y old), and

6 to 16 subadult females (under 12 y old). Birthdates are known to within 1 mo for all immature individuals included in this study.

Data Collection and Analysis.

Aggressive experience. First, we used all-occurrence aggression from the KCP (2005 to 2017) to examine early life aggressive experience. During each day of KCP data collection, researchers and field assistants worked in teams to conduct observational follows of chimpanzee parties. At 15-min intervals throughout each day, observers recorded party composition scans including the identity of all individuals within 50 m of each other. Observers recorded all occurrences of aggression in the party, which is made possible by the conspicuous nature of chimpanzee agonism. Aggressive behaviors included charging displays (both vocal and nonvocal), chases, and attacks, defined as any instances of aggression that involved bodily contact (following ref. 48, described in detail in refs. 52 and 68). For each aggressive behavior and/or interaction, observers recorded the identity of the aggressor and any targeted victims, as well as a detailed description of the aggressive behaviors displayed and any responses by victims or other party members. A total of 59,751 aggressive incidents were recorded over the course of the study, and 27,669 of those were targeted at one or more victims.

We extracted data from individuals under 9 y old to capture variation in aggressive experience that occurs before pubertal surges in gonadal hormones (n = 49, f = 25, m = 24) and considered two elements of aggressive experience. First, exposure to aggression included all instances of aggression that occurred in the party while a given immature chimpanzee was present, whether or not there was a specific, targeted victim. We considered this separately from aggression directly received by immature chimpanzees, which included all instances that a given immature chimpanzee was clearly the direct target for aggression by another individual (see *SI Appendix*, Table S1 for descriptive and summary statistics). We tabulated exposure to aggression among other group members and aggression directly received by each immature in half-year age intervals from birth to 9 y.

We used generalized linear mixed models (*glmm*, glmmTMB ver.0.2.3, 69) to identify and characterize any sex differences in the amount of aggression that young chimpanzees were exposed to and directly received during development. For both models, our response variable was a count of aggressive events and both response variables were right skewed. We therefore modeled each using a negative binomial error distribution and adjusting for zero inflation where appropriate (see *SI Appendix* for further details). Observation hours, calculated from party composition scans, were included as an offset term in both models. We included sex, age, and their interaction as fixed effects in each model. As wild primate studies have previously reported significant effects of mother's rank on early social experience, including aspects of aggression (i.e., refs. 70, 71), we included mother's rank in each initial model and allowed it to interact with age and sex. Interaction terms that were both not significant and did not improve model fit were removed from the model (see *SI Appendix* for additional details). Finally, we included individual identity nested within mother's identity as random effects to account for unequal sampling of individuals and the inclusion of maternal siblings in the sample.

Other contributing early life social factors. Second, KHS used 2-h focal follows of immature chimpanzees with 15-min scan intervals (n = 25, females = 14, males = 11) to collect detailed spatial data over three seasons from January to August of 2015, 2016, and 2017 (see *SI Appendix*, Table S2 for summary statistics). We used *glmms* (glmmTMB ver.0.2.3, 69) to identify sex differences in four aspects of early sociality that may, in turn, contribute to sex differences in aggressive exposure. As before, our response variables comprised count data and we adjusted our modeling approach to account for zero inflation and overdispersion as necessary (see *SI Appendix* for further details). [P1] Exposure to adult males was measured as the number of scans during each focal follow that the focal immature was found in a party with at least one adult male. [P2] Time spent in close proximity to adult males was measured as the number of scans that focals were found within 5 m of at least one adult male partner, given that one was available in the party. [P3] Spatial independence from mothers was measured as the number of scans during which focals were farther than 5 m from their mothers. Each measure was tabulated for each 2-h focal follow, which comprised the unit of analysis, and each model included offset terms for the number of eligible scans in the follow (see *SI Appendix* for specific details by model). Age was calculated on the day of each follow. Finally, [P4] we drew from the long-term aggression records from KCP, as above, to investigate differences in the use of aggression by immature male and female chimpanzees (offset by hours observed, as before). We included age, sex, and mother's rank as main effects in all analyses, as well as random effects of individual nested within mother. As before, we initially included interactions between main effects in each model but removed them to simplify the model if they were both nonsignificant and did not improve model fit (see *SI Appendix* for details).

Integrated model of aggressive experience and early sociality. Finally, we used multivariate modeling to directly examine how aspects of individuals' social lives contributed to the amount of aggression they received. For this analysis, we calculated average exposure to adult males, proximity to available adult male partners, spatial independence, and the rate of aggression displayed per hour observed for each focal chimpanzee (n = 25, f = 14, m = 11) during each of the three study periods (January to July 2015, 2016, and 2017), and examined these, along with age, sex, and maternal rank, as predictors of the amount of aggression received during the same period. While our inclusion of each predictor was theoretically justified and collinearity analysis revealed that all main effects satisfied assumptions of independence (*performance* ver. 0.4.6) (72), we expected that predictors could interact with one another, leading to large numbers of predictors and overly complicated models. Thus, we used a multimodel selection procedure (*MuMin* ver. 1.43.15) (73, 74) to narrow down our full model and identify the combination of those social variables (including interaction terms) that best-predicted aggression received without overfitting (see *SI Appendix* for further details).

Outliers. Initial visual inspection indicated a few possible outliers with potential effects on our results. Therefore, we repeated all analyses excluding those observations. The results from these models were not meaningfully different from those with a full dataset. As such, we report the analysis using the full data here (see *SI Appendix* for further details).

Results

Males Are Exposed to More Aggression. Per hour observed, males were exposed to slightly but significantly more aggression among other group members than were females (*glmm*, intercept [Int] = -1.227 ± 0.11, $P < 0.001$, $\beta = 0.291 \pm 0.07$, $P < 0.001$, Fig. 1*A* and *SI Appendix*, Table S3), and there was no relationship between exposure to aggression and age ($\beta = -0.013 \pm 0.01$, $P = 0.34$) or mother's rank ($\beta = -0.205 \pm 0.14$, $P = 0.15$). There was a more pronounced difference in the amount of aggression that males and

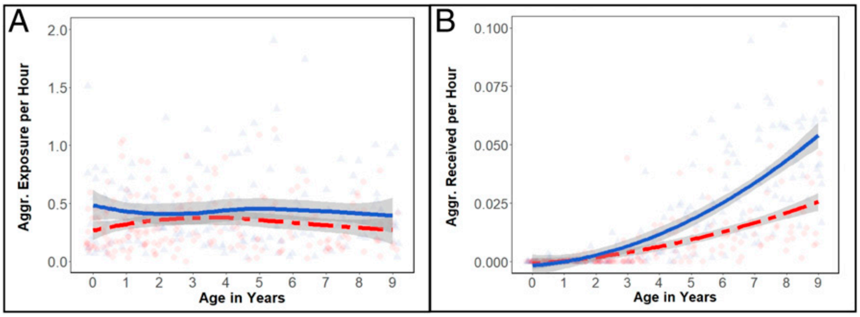

Fig. 1. Sex differences in aggressive exposure and aggression directly received during development. Immature males (n = 24) both (*A*) witnessed, and (*B*) directly received more aggression per hour observed compared to females (n = 25) during development. Females are shown in red (circles and dashed lines) and males in blue (triangles and solid lines).

females received. Immature chimpanzees—primarily juveniles (5 to 9 y old)—were victims in 3,082 cases of targeted aggression (11% of all targeted aggression). Both sexes received more aggression with age (*glmm*, Int = -5.995 ± 0.32, $P < 0.001$, $\beta = 0.273 \pm 0.05$, $P < 0.001$, Fig. 1*B* and *SI Appendix*, Table S3), and age interacted with sex such that the increase was greater among males compared to females ($\beta = 0.115 \pm 0.06$ $P = 0.04$), leading males to receive more aggression than females by about 4–5 y old.

Most of the aggression received by immature chimpanzees came from adult males (Fig. 2 and *SI Appendix*, Table S4, $n = 979$, 31.7%), nonmother adult females ($n = 816$, 26.5%), and adolescent males ($n = 502$, 19.5%). When considering the sex of the victim, compared to young females ($n = 304$, 25%), young males received more aggression from adult males ($n = 669$, 36%). More aggression directed at young females came from subadults, especially juvenile males ($n = 152$, 12.5% compared to $n = 105$, 5.7% for young male victims). While mothers almost never used aggression against their offspring ($n = 85$, 2.8%), more maternal aggression was directed at males ($n = 71$) compared to females ($n = 14$).

Sex Differences in Early Sociality. Next we investigated whether sex differences in other aspects of social development put males at higher risk of receiving aggression (see *SI Appendix*, Table S3 for results from all models). There was no significant difference in the frequency with which immature females and males were found in parties with at least one adult male (Fig. 3*A*) or in the amount of time that young males and females spent in close proximity to adult males (Fig. 3*B*). While there was a sex difference in time spent beyond 5 m from mothers, it was opposite to the direction predicted. While all infants and juveniles spent more time outside of their mothers' 5-m proximity as they aged (Fig. 3*C*, *glmm*; Int = -3.957 ± 0.24, $P < 0.001$, $\beta = 0.467 \pm 0.04$, $P < 0.001$), males were slightly but significantly less likely to do so than females ($\beta = -0.642 \pm 0.32$, $P = 0.04$). Finally, we investigated the possibility that males may have received more aggression than females because they were aggressive themselves. Both sexes displayed aggression more frequently as they aged (Fig. 3*D*, *glmm*; Int = -1.414 ± 0.310, $\beta = 0.530 \pm 0.056$, $P < 0.001$). However, increases were stronger among males compared to females ($\beta = 1.112 \pm 0.086$ $P < 0.001$). By age 5 to 6 y, males displayed more aggression than females. This overlapped with the time in development that males began receiving more aggression. Mother's rank was not significantly associated with any of these aspects of early sociality.

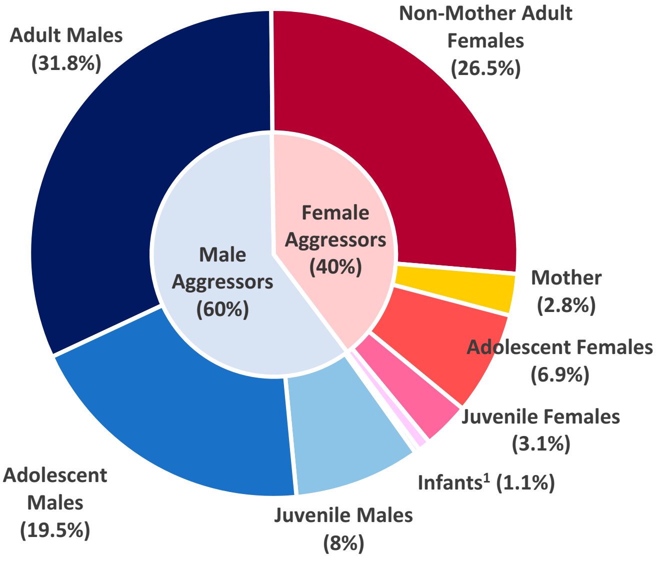

Fig. 2. Sources of aggression against immature chimpanzees. Overall, infants and juveniles received aggression more often from males ($n = 1{,}848$) than from females ($n = 1{,}284$). Adult males ($n = 979$), nonmother adult females ($n = 816$), and adolescent males ($n = 602$) represented the largest sources of aggression, respectively, against immature chimpanzees. Infant aggressors included both males and females.

Sources of Variation in Aggressive Exposure. Our model selection procedure identified 11 plausible top models to explain individual differences in early aggressive experience. These models were qualitatively similar in that they shared a relatively stable set of predictors and differed in Akaike information criterion (AIC) by <5 (*SI Appendix*, Table S5; 74). In every model, the strongest predictor of how much aggression an infant or juvenile received was the amount of aggression they displayed. Neither a main effect of sex nor any potential interactions between sex and early life sociality were included in any of the top 11 models (*SI Appendix*, Table S5). This indicates that, after controlling for other predictors, including sex does not improve model fit. As the Akaike weight of the top model was nearly twice that of the next-best model, indicating that it is twice as likely to be the best model (74), we report the results of that model here (Fig. 4).

Immature chimpanzees that received more aggression were those that displayed more aggression (*glmm*; Int = -4.616, $\beta = 2.694$, $P < 0.001$). However, this effect interacted negatively with age ($\beta = -1.308$, $P < 0.001$). Thus, as chimpanzees grew older, they received less aggression relative to the aggression that they displayed. While increasing independence from mothers was associated with receiving more aggression ($\beta = 0.499$, $P = 0.03$), this effect also diminished, or negatively interacted, with increasing age ($\beta = -0.431$, $P < 0.01$). Independent of other factors, aggression received also increased with age ($\beta = 0.830$, $P < 0.01$). Finally, counter to our prediction that spending time in parties with adult males would be risky, immature individuals that spent more time in parties with adult males actually received less aggression ($\beta = -0.993$, $P = 0.02$).

Discussion

Our investigation of development under natural conditions revealed that immature male chimpanzees experienced significantly more physical aggression than immature females. Overall, immature chimpanzees received far less aggression than adults (11% of all aggression). However, immature males received aggression three times more often than females by 5 y old. By contrast, there was only a small difference in the amount of aggression that immature males and females were exposed to that occurred among individuals other than themselves. This amounted to young males being exposed to one additional aggressive interaction per 3.4 h of observation, on average. This pattern was not explained by males spending more time in parties with or in close proximity to adult males. Rather, aggression displayed was the strongest predictor of aggression received, and young males displayed more aggression than females. Remarkably, despite robust sex differences in receiving aggression during the juvenile period, we found no independent effect of sex in multivariate analyses. Instead, the sex difference in aggressive experience was apparently mediated through differences in social behavior. Taken together, this evidence indicates that young male chimpanzees were targeted for aggression not because of their maleness, per se, but because, as males, they were more likely to exhibit behaviors that elicit aggression. Our data are thus consistent with the hypothesis that, in chimpanzees, sex differences in aggression emerge early in development, without the influence of gender socialization. This suggests the need to explore factors other than active socialization that may contribute to the early emergence of sex differences in human

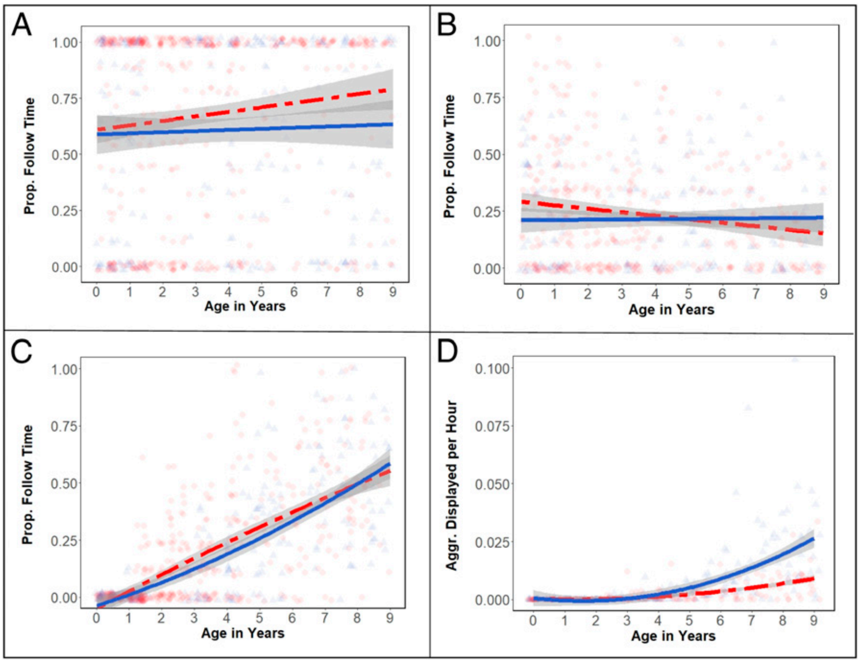

Fig. 3. Early life sociality across development for males and females. In all panels, females are shown in red (circles and dashed lines) and males are in blue (triangles and solid lines). *A*–*C* represent data collected during a targeted social development study (January through August 2015, 2016, 2017, unique IDs = 25, f = 14, m = 11) including the proportion of each focal follow spent (*A*) in parties with at least one adult male, (*B*) within 5 m of an adult male given that one was available, and (*C*) farther than 5 m from their mother. *D* shows aggression displayed per hour observed by age and sex using long-term aggression data (2005 to 2017, unique IDs = 49, f = 25, m = 24). For ease of interpretation, all panels display raw data rather than model results.

physical aggression, including intrinsic biological factors and social experience (9, 10, 75).

Juvenile male macaques and baboons similarly receive more aggression as they begin to compete with other group members for status (41–43). Thus, the experience of receiving more aggression corresponds with displaying aggression across multiple taxa. In many species, behavioral and hormonal development coalesce such that increasing male aggression coincides with puberty and associated surges in testosterone (29, 76). Wild chimpanzees similarly begin competing for status as they reach reproductive maturity (77). However, a small study of captive chimpanzees living in peer-only groups found that males with higher testosterone for their age had higher rank and, consequently, were both more likely to display aggression and less likely to receive aggression even before puberty (28, 78). In this study, we detected increases in males' use of aggression as early as 5 to 6 y old. This suggests that behavioral changes occur even very early in puberty, when testosterone levels are rising but still low (28, 78–80).

Early-life androgens other than testosterone could also impact aggressive development through independent organizational effects on prenatal brain development (29, 81). These pathways, which are thought to be activated by testosterone during puberty, may also be activated during adrenarche (82), a prepubertal developmental milestone that marks the maturation of the adrenal gland and is accompanied by increases in the adrenal androgen dehydroepiandrosterone (DHEA) and its sulfate (DHEAS, denoted jointly as DHEA/S) (83). In both captivity (84, 85) and our study population of wild chimpanzees (86) increasing DHEAS is detectable several years prior to puberty. Although its effects are weaker than testosterone, DHEA/S is associated with increased aggression in birds and mammals (87). While male and female chimpanzees exhibit similar DHEAS levels throughout development (86), this abundant androgen hormone could still contribute to developmental increases in aggression among chimpanzees by activating prenatally organized differences in neural pathways (29, 81, 82).

Against our expectations, individuals that spent more time in parties with adult males actually received less aggression. Further, only 32% of aggression directed at infants and juveniles came from adult males. Thus, exposure to adult males could be less risky than previously thought or is only risky for the youngest infants (62, 63). Our findings could also be explained by familiarity, as evidence suggests that mothers' close male associates are less aggressive toward offspring (88, 89). Additionally, adult male presence may have a pacifying effect on interactions among other group members as high-ranking adult males police aggression between other group members, especially those that they outrank (61, 90). As more than half of aggression against infants and juveniles came from nonmother adult females and adolescent males—those individuals most affected by policing from adult males—spending time in parties with familiar adult males could actually shield infants and juveniles from aggression.

Unlike macaques and baboons, where a significant portion of aggression toward immature individuals comes from their own mothers (40, 43), chimpanzee mothers were almost never aggressive toward their offspring. In fact, although immature males received over five times more aggression from their mothers than did immature females, aggression from mothers was so infrequent that we could not statistically investigate sex differences.

In some, but not all, female-philopatric monkeys, increased aggression toward young males has been attributed to male dispersal patterns, as targeting young males for aggression may hasten emigration before they become serious competitors for mates (43). Immature chimpanzee males experience the same pattern of increased aggression, but dispersal is biased toward females, indicating that dispersal patterns do not explain early aggressive experiences among chimpanzees.

As expected, young chimpanzees gained independence from their mothers with age, and individuals that spent more time out

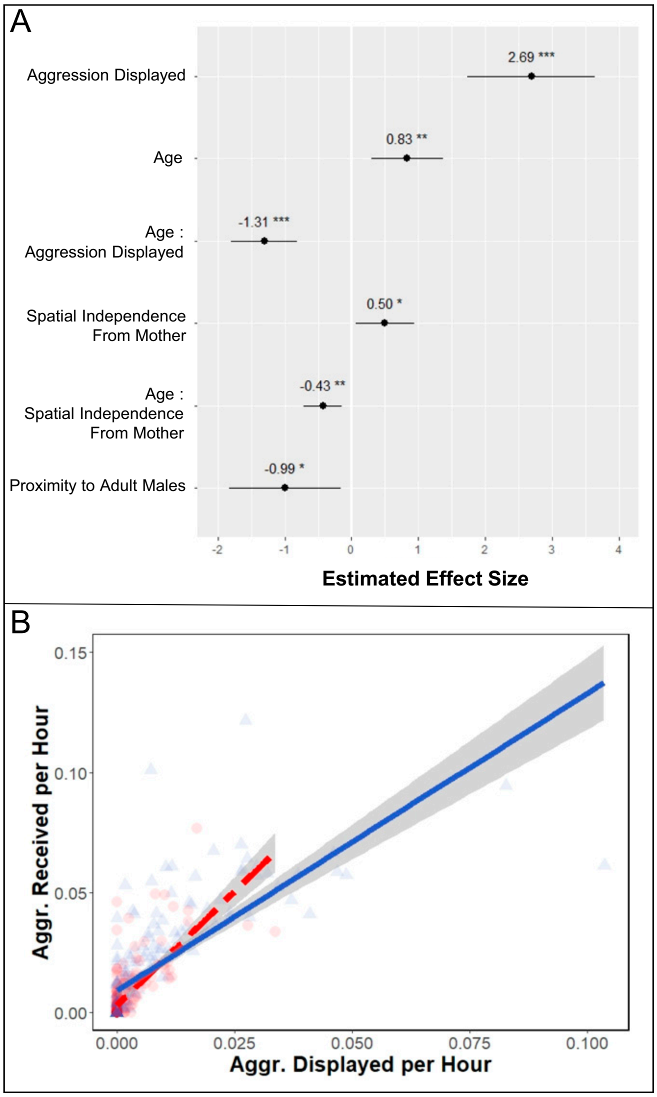

Fig. 4. (*A*) Estimates and their SE for each model parameter included in the best fit model. Asterisks (*) denote the significance of each effect (*$P < 0.5$, **$P < 0.01$, ***$P < 0.001$). (*B*) Aggression displayed was the strongest predictor of how much aggression immature individuals received in every plausible model. Shown here using raw data from the full aggression dataset (2005 to 2017, $n = 49$, f = 25, m = 24). Females are shown in red (circles and dashed lines) and males are in blue (triangles and solid lines).

of close proximity to their mothers received more aggression. However, this effect diminished with age. Additionally, in contrast to our expectations, young males at Kanyawara did not spend more time out of close proximity from mothers compared to females of the same age. Taken together, our results may indicate that independence is especially risky among younger, less experienced, individuals. Alternatively, early experience of aggression may feed back on social independence during development, causing those chimpanzees that receive a lot of aggression to spend more time near their mothers for social support and/or in attempts to avoid further aggression.

Our results document clear differences in the aggressive experiences of young chimpanzees. This finding supports the possibility that early life experiences may help to shape sexually dimorphic behavioral patterns in the absence of explicitly taught cultural gender norms. However, young males were not simply collateral damage as a consequence of party affiliation or proximity, nor were they targeted specifically because they were male. Instead, their own physically aggressive behavior provoked aggressive responses from others. This evidence suggests that male chimpanzees are more inclined to physical aggression as juveniles than are females, a pattern that has received broad support from studies of social play across primates (30, 33, 91). Thus, while differences in early life exposure to aggression were ostensibly structured in a way that could precipitate sex differences in the use of aggression later in life, these experiential differences were influenced by early-emerging differences in social behavior that already resembled adult patterns. While our results may not directly apply to humans, they underscore the importance of probing alternative and complementary experiential mechanisms, especially learning versus active teaching, that may interact with socialization to shape behavioral patterns during child development.

Ethical Approval. Data collection and procedures followed all applicable international, national, and institutional guidelines. Local permissions were granted by the Uganda Wildlife Authority, the Uganda National Council of Science and Technology, and Makerere Biological Field Station. All procedures in this study were approved in accordance with the ethical standards of the University of New Mexico Institutional Animal Care and Use Committee (no. 19–200862-MC).

Data Availability. Data analyzed in this study are available on Dryad (92).

ACKNOWLEDGMENTS. Long-term data collection was performed by a team of Ugandan field assistants including the late John Barwogeza, Sunday John, Christopher Katongole, J. Kyomuhando, Francis Mugurusi, the late Donor Muhangyi, the late Christopher Muruuli, Solomon Musana, Japan Musunguzi, Dennis Sebugwawo, Peter Tuhairwe, James Kyomuhendo, Wilberforce Tweheyo, Richard Karamagi, Seezi Atweijuze, Daniel Akaruhanga, Fred Baguma, Steven Alio, and Bashil Musabe. Maggy Kobusingye, Christine Abbe, and Jovia Mahoro assisted with data collection and management in the field. Ashley Menante and Jordan Lucore managed the long-term database and organized data. Drew Enigk helped to clean aggression data and calculated dominance scores for the mother chimpanzees included in this study. We thank Elizabeth Lonsdorf for her feedback on previous versions of this manuscript and are grateful to two anonymous reviewers for their helpful comments. Funding for fieldwork by the Kibale Chimpanzee Project and for hormonal assays has been provided by the NSF (grants 1355014, 9807448, 0416125, 1926653, and NCS-FO-1926352), the National Institute on Aging and Office for Research on Women's Health (NIH grant R01-AG045395), the L.S.B. Leakey Foundation, the Wenner-Gren Foundation, the Nacey Maggioncalda Foundation, the American Philosophical Society, Harvard University, and the University of New Mexico.

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