

Development of socio-emotional competence in bonobos

Zanna Clay¹ and Frans B. M. de Waal¹

Living Links, Yerkes National Primate Research Center, Emory University, Atlanta, GA 30322

Contributed by Frans B. M. de Waal, August 31, 2013 (sent for review June 14, 2013)

Social and emotional skills are tightly interlinked in human development, and both are negatively impacted by disrupted social development. The same interplay between social and emotional skills, including expressions of empathy, has received scant attention in other primates however, despite the growing interest in caring, friendships, and the fitness benefits of social skills. Here we examine the development of socio-emotional competence in juvenile bonobos (*Pan paniscus*) at a sanctuary in the Democratic Republic of the Congo, focusing on the interplay between various skills, including empathy-related responding. Most subjects were rehabilitated orphans, but some were born at the sanctuary and mother-reared there. We observed how juveniles with different rearing backgrounds responded to stressful events, both when the stress affected themselves (e.g., a lost fight) or others (e.g., witnessing the distress of others). The main dependent variable was the consolation of distressed parties by means of calming body contact. As in children, consolation was predicted by overall social competence and effective emotion regulation, as reflected in the speed of recovery from self-distress and behavioral measures of anxiety. Juveniles more effective at self-regulation were more likely to console others in distress, and such behavior was more typical of mother-reared juveniles than orphans. These results highlight the interplay between the development of social and emotional skills in our ape relatives and the importance of the mother-offspring bond in shaping socio-emotional competence.

social deprivation | sympathetic concern | emotional control | personal distress

Socio-emotional competence encompasses an array of skills, such as successfully forming and maintaining social relationships, behaving appropriately in social situations, being sensitive to the emotions of others, and effectively managing one's own emotions (1). Emotion regulation (ER) is an essential part of socio-emotional competence and is defined as the process of modifying, inhibiting, evaluating, and monitoring internal states and reactions to enable an individual to adaptively respond to arousing situations so as to achieve individual goals (1, 2). Throughout development, social and emotional skills are tightly interconnected and "people who are unable to modulate the intensity and duration of their internal emotional responses and emotionally driven behavior are likely to be physiologically over-aroused and to behave in ways that do not foster constructive social interactions" (3).

Studies of child development show that effectively managing one's own emotions allows for greater empathy with others, including caring responses known as *sympathetic concern* (4–6). Sympathetic concern interacts with other social skills that emerge across development, including perspective-taking (5–9). It is reliably predicted by ER, with low-regulating individuals more likely to become emotionally overwhelmed when exposed to another's distress, resulting in a more self-centered *personal distress* (6, 8, 9). This connection develops at an early age: infants with signs of better ER show less personal distress in response to peer cries than those with poorer ER (10). Overall, socially competent behavior, which includes expressions of sympathy and prosocial behavior, as well as socially appropriate responses and

popularity, reliably relates to better ER in children and adults (1–3, 7–11).

This socio-emotional framework is rarely applied to other species, however. This is curious, because if it is critically important for humans one would expect it to also apply to some degree to our closest relatives, the anthropoid apes. To explore this issue, we measured purported markers of socio-emotional competence in young bonobos along with consolation behavior, which previous research has suggested to be a marker of sympathetic concern (12–14). Consolation is defined as spontaneous contact comfort aimed at distressed parties by means of touching, stroking, embracing, and kissing (15) (Fig. 1), a behavior well-known of both children and apes (4–6, 12–16). In human children, consolation behavior appears already in the first year of life (10, 17), suggesting that although the cognitive component of empathy increases across development, it is no prerequisite for expressions of concern. ER seems to be critical: infants without effective ER do not orient to others because they cannot overcome their own personal distress in the face of another's distress (10, 18).

Whereas few animal studies have explicitly addressed ER, experimental research has revealed relevant similarities. For example, primates and other animals show human-like skin conductance and heart rate responses to emotionally arousing or calming stimuli (19–23). Chimpanzees (*Pan troglodytes*) spontaneously match images of positive vs. negative facial expressions to videos depicting pleasant vs. aversive situations, suggesting awareness of the emotional connotations of their species' facial displays (19). Studies addressing emotional control typically adopt a deferred gratification paradigm. Apes, and to a lesser extent monkeys and nonprimates (24–26), are able to control the

Significance

Across human development, individuals better able to manage their own emotions show greater social competence and more empathic concern for others. To test this interplay between social and emotional skills in one of our closest relatives, we collected behavioral measures on bonobos (*Pan paniscus*) with different rearing backgrounds at a forested sanctuary in Africa. Young bonobos showed the same connection between the ability to regulate their own emotions and social competence, such as developing friendships and concern for others. Mother-reared juveniles performed far better in this regard than juveniles orphaned at a young age, thus highlighting the importance of the mother-offspring bond. Our results support a shared socio-emotional framework for human and non-human primate behavior.

Author contributions: Z.C. and F.B.M.d.W. designed research; Z.C. performed research; Z.C. and F.B.M.d.W. contributed new reagents/analytic tools; Z.C. and F.B.M.d.W. analyzed data; and Z.C. and F.B.M.d.W. wrote the paper.

The authors declare no conflict of interest.

¹To whom correspondence may be addressed. E-mail: zannaclay@emory.edu or dewaal@emory.edu.

This article contains supporting information online at www.pnas.org/lookup/suppl/doi:10.1073/pnas.1316449110/-DCSupplemental.

urge to reach for a reward if holding back increases the chance of a better reward later on. Moreover, like children, apes seek to distract themselves in an apparent attempt to control the temptation of immediate gratification (26). Such research suggests the importance of ER for ape behavior.

An area with significant overlap in human and nonhuman developmental research is that of social deprivation. Socially deprived children demonstrate poor emotional and social competence, including lower sympathetic concern, increased risk for psychiatric disorders, and enlarged amygdala volumes, indicative of high anxiety (27–30). Although adoptive care can mitigate these negative effects, orphaned children typically show lasting socio-emotional disruptions (30). Similar effects of early deprivation have been documented in chimpanzees, rhesus monkeys (*Macaca mulatta*), and other primates, including increased anxiety, an inability to develop social relationships, lack of recognition of social signals, and stereotypical behaviors (31–36). A study of socially deprived monkeys found a deficiency in species-typical reconciliation with opponents after conflict, which is an essential social skill (34, 36). Although some negative effects of social deprivation can be overcome, this mostly applies to deprivation later in development, such as after weaning, or after having received substitutive maternal care (37, 38).

Bonobos at a forested African sanctuary offered an opportunity to measure many of these variables in both mother-raised and orphaned juveniles, thus allowing a test of predictions derived from the above studies. Most study subjects were wild-caught orphans rescued from the illegal bush-meat and pet trades and subsequently rehabilitated with the help of human mother substitutes. The bonobo is a species of particular interest given its close genetic similarity to our own (39) and its reputation of social tolerance, peacefulness, and reduced levels of violence compared with its congener, the chimpanzee (40). Bonobos also seem to have high empathy levels (41) and are equipped with the neural substrate to support these tendencies (42). Consistent with empathy-based predictions (43), our previous study found consolation to be typical of closely bonded individuals, both kin and nonkin. Both reconciliation between former opponents and consolation of distressed parties occurred across all age classes, highlighting successful social rehabilitation within the sanctuary environment. Nevertheless, mother-reared juveniles were significantly more likely to offer consolation to others than orphans of any age (44).

A year after our first study, we observed the same bonobo juveniles in greater detail to investigate the interplay between socio-emotional competence at baseline while experiencing self-distress (i.e., as a victim of a fight), and in response to the distress of others (i.e., as a bystander to conflict). Our main dependent variable was spontaneously offered consolation after naturally occurring aggressive and/or stressful episodes. We predicted that juvenile bonobos scoring higher on measures of overall sociality and socio-emotional competence, including ER, would be more likely to console distressed parties. We evaluated these effects using a generalized linear mixed model (GLMM), which helps determine independent contributions, controlled for age, sex, and other factors.

Results

Responses to Others' Distress. A total of 373 postdistress (PD) periods were recorded (i.e., 318 postconflict focals and 55 tantrum responses), which were all included in the analysis (*Methods*). The mean percentage of consolation across age, sex, and rearing classes was compared (i.e., number of PD periods in which a given bystander offered consolation divided by the number of PD events witnessed). Replicating previous results (44), the probability of offering consolation was significantly affected by bystander age category ($n = 13$ adults, $n = 11$ adolescents, $n = 12$ juveniles; Kruskal-Wallis χ^2 on percent consolation

offered = 9.47, $df = 2$, $P = 0.009$, two-tailed, and henceforth two-tailed in all analyses). Juvenile bystanders were more likely to console than adults (Mann-Whitney $U = 29.5$, $P = 0.007$, exact probability, and henceforth all paired analyses; Table 1) or adolescents ($U = 23.0$, $P = 0.007$; Table 1), but there was no significant difference between adults and adolescents ($P > 0.05$). Mother-reared juveniles were almost three times more likely to console victims than were orphaned juveniles (Mann-Whitney $U = 2.0$, $P = 0.009$; Table 1). No significant effects of sex were found.

A similar analysis tested whether the distressed individuals themselves sought contact differently with bystanders in these categories, but no significant differences in frequency were found, either between the three age categories or with regard to rearing background. A within-subjects analysis of the rate of offered consolation to distressed parties compared with the rate with which these parties sought contact from the same bystander revealed that mother-reared juvenile bystanders offered almost three times as many contacts than they received (Wilcoxon signed ranks test: $Z = -2.02$, $P = 0.043$; Table 1). No such within-subject difference was found for orphaned juveniles ($Z = -0.54$, $P > 0.05$). In other words, age and rearing affected the bystander's active response to another's distress, but not the number of contacts received.

Whereas the above analyses only considered positive affiliative contacts made with the victim, negative responses were also analyzed. The immediate responses of juvenile bystanders within 3 m at the onset of the PD event were compared. A Positive Response Index (PRI; *Methods*) per individual took into account all immediate positive (i.e., approach/contact) and negative or avoidant responses (flee/move away/scream). $PRI = (P - N) / (P + N)$, in which P is the number of PD periods with a positive response and N the number with a negative response. Neutral or unclassifiable responses (e.g., sitting, staying) were ignored. Mother-reared juveniles showed a dramatically higher mean PRI than orphans, which were far more avoidant (i.e., showed a negative PRI) (mean PRI \pm SD for mother-reared juveniles ($n = 6$): 0.15 ± 0.29 vs. orphan juveniles ($n = 6$): -0.75 ± 0.22 ; Mann-Whitney $U = 0.0$, $P = 0.002$).

ER: Overcoming Self-Distress. The human developmental ER literatures suggest a relation between (i) regulating one's own distress and (ii) offering comfort to others, with orphans being poorer at both. First, we examined how juveniles with differing rearing backgrounds responded to the distress they experienced directly as victims during PD periods. Although there were no significant rearing effects on the mean duration of victim screams in both $n = 6$ categories of juveniles (Mann-Whitney $U = 9.0$, $P > 0.05$; Table 2), mother-reared juveniles were significantly less likely than orphans to recommence screaming once their vocalizations had stopped for 30 s or longer (Mann-Whitney $U = 2.5$, $P = 0.009$; Table 2). Mother-reared juveniles recovered sooner than orphan juveniles, as also indicated by the shorter latency to cease anxiety-related behaviors (Mann-Whitney $U = 0.0$, $P = 0.002$; Table 2). *SI Text* provides separate analyses of PD events

Table 1. Mean (+SD) percentage of events each bystander offers consolation to a victim compared with receiving contact from the victim

Bystander age	Response to victim	
	Offer consolation	Receive contact
Adult	2.56 (1.57)	3.19 (2.09)
Adolescent	2.74 (2.65)	2.84 (3.98)
Juvenile orphan	4.14 (2.80)	3.24 (1.22)
Juvenile mother-reared	11.41 (5.14)	3.09 (1.57)

Table 2. Mean values (+SD) of measures of self-distress by victims during PD periods

Measures of self-distress	Juvenile rearing	
	Mother-reared	Orphan
Scream duration, s	6.5 (3.0)	10.2 (4.0)
Recommence scream, % of events	10.0 (6.0)	44.0 (5.0)
Latency to recover, s	27 (26.0)	130 (27.0)

Scream duration: duration of the first uninterrupted screaming episode. Recommence scream: percentage of PD periods in which the victim recommences screaming once their vocalizations have stopped for >30 s. Latency to recover: mean latency to cease anxiety-related behaviors.

with and without consolation, both showing significant effects in the same direction. Consistent with the ER framework, a Spearman correlation revealed a solid relationship across individuals between faster recovery as a victim and offering consolation to others as a bystander (i.e., latency to cease anxiety responses as victim vs. the probability of offering consolation as a bystander: Spearman's $\rho = -0.70$, $n = 12$, $P = 0.012$).

Second, we collected baseline rates of self-scratching [a behavioral marker of anxiety (9, 10)] as an additional measure of ER (45). Mother-reared juveniles showed only half the baseline rate of self-scratching compared with orphaned juveniles (mean rate of self-scratching per minute: mother-reared = 0.10 ± 0.05 ; orphan = 0.20 ± 0.08 , $U = 5.0$, $P = 0.035$; Fig. 2).

Social Competence: Sustained Play and Friendships. The mean length of play bouts, thought to reflect sustained friendly social interaction, was significantly higher for mother-reared juveniles compared with orphans (mean duration of play episode: mother-reared = 141 ± 23 s, orphan = 98 ± 35 s, Mann-Whitney $U = 5.5$, $P = 0.041$). Mother-reared juveniles also spent more than twice as much of their time engaged in social play compared with orphans (Fig. 2; $U = 4.0$, $P = 0.024$) and initiated play interactions with others more than twice as frequently compared with orphans (Fig. 2; $U = 2.0$, $P = 0.009$). Mother-reared juveniles had three times as many friends (closely bonded partners, i.e., dyads with affinity scores within the upper quartile) (Fig. 2; $U = 2.0$, $P = 0.011$). The sociality data for mother-reared juveniles excluded any interactions with their own mothers (*Methods*), further emphasizing their greater sociality compared with orphans, despite their overall sociality being undermeasured.

Composite Sociality Index. A Composite Sociality Index (CSI) (46) was constructed to examine the relationship between sociality, a sign of general social competence, and an individual's response to self-distress and other-distress. Mother-reared individuals showed significantly higher CSI scores than orphans (Mann-Whitney $U = 2$, $P = 0.010$), and an individual's CSI correlated highly with its tendency to offer consolation to others as a bystander (CSI * percent offered consolation: $\rho = 0.82$, $n = 12$, $P = 0.001$; Fig. 3). Consistent with the socio-emotional competence framework, CSI also correlated with faster recovery from anxiety as a victim (CSI * latency to cease anxiety responses as victim: $\rho = -0.72$, $n = 12$, $P = 0.008$).

Factors determining consolation by juvenile bystanders were examined using a GLMM, which included the CSI as independent variable. All possible models were compared using the Akaike information criterion (AIC), which identifies the most parsimonious model to explain the variance of the dependent variable. The best-fitting model, which fits significantly better to the data than the null model ($P < 0.001$), included two uncorrelated variables, bystander CSI and the degree of baseline affiliation between bystander and victim (AIC = 912.53, $\chi^2 = 14.33$, $df = 1$, $P < 0.001$). Juveniles high on sociality (CSI) were more likely to

console others (CSI: $\beta = 1.426$, $SE = 0.29$, $Z = 4.85$, $P < 0.001$), and bystanders were more likely to console victims with whom they shared a close affiliative relationship (Affiliation: $\beta = 0.043$, $SE = 0.018$, $Z = 2.38$, $P = 0.017$). The next best model included bystander rearing in addition to CSI and bystander-victim affiliation (AIC = 913.31, $\chi^2 = 1.21$, $df = 0$, $P < 0.0001$), with mother-reared juveniles more likely to console than orphans, although not significantly so ($\beta = 0.39$, $SE = 0.37$, $Z = 1.06$, $P = 0.29$). Although rearing and CSI were positively correlated (0.72), the highest Variance Inflation Factor (VIF) between them was less than 10 (VIF of rearing = 2.476), suggesting this competing model can be considered. Nevertheless, the model containing affiliation while replacing CSI with rearing fitted less well (AIC = 916.36, $\chi^2 = 0.66$, $df = 0$, $P < 0.0001$), compared with the model containing CSI.

Discussion

Juvenile bonobos with signs of better social and emotional competence were more likely to respond to the distress of others by offering consolation. There was a direct positive correlation between how juveniles handled their own distress events as victims and how they responded to distress witnessed in others: individuals quicker to recover from their own distress as victims were more likely to provide bodily comfort to others. Individuals with higher sociality (expressed in the CSI, a marker of overall social competence) were most likely to offer consolation and approach victims rather than fleeing (expressed in the PRI). In agreement with human infant studies (45, 47), sociality was the best predictor of consolation behavior. Consistent with empathy-



Fig. 1. One juvenile bonobo embraces a distressed companion during postconflict consolation. Photograph by Zanna Clay at the Lola ya Bonobo Sanctuary in the Democratic Republic of the Congo.

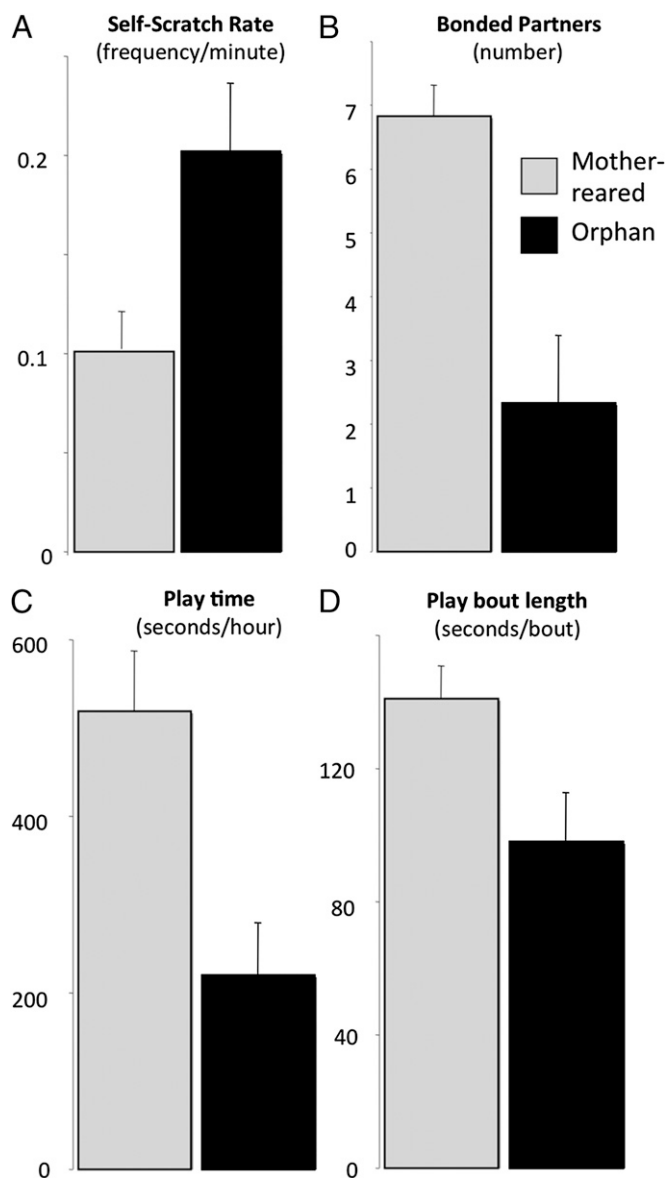


Fig. 2. Bar charts of the mean + SEM of (A) one emotion regulation measure and (B–D) three social competence measures for orphan ($n = 6$) and mother-reared juveniles ($n = 6$) during baseline focal periods: (A) rate of self-scratching per minute, (B) number of closely bonded partners per individual (excluding mother-offspring relationships), (C) duration of time spent playing (seconds per hour), and (D) length of average play bout (duration per bout, in seconds).

based predictions (43), the affiliative relationship between bystander and victim was also a significant predictor.

We replicated our previous finding (44) that juvenile bonobos consoled more than adults or adolescents. Although seemingly at odds with the human literature (4, 6, 48), the findings suggest that juveniles react to the emotions of others but may not yet possess the cognitive filters, compared with adults, who evaluate the situation and are more inhibited and discriminating (48). It is hard to make meaningful interspecies comparisons in this regard, however, because the methodology typically used for adult human studies (i.e., questionnaires) differs markedly from the observational measures applied to children and used here.

One of our main independent variables is rearing background, known to affect the development of socio-emotional competence in humans. We found that mother-reared juveniles were more

likely than orphans to console victims, more likely to recover quickly from distress as victims themselves, and scored higher on social competence and lower on anxiety (as measured by baseline self-scratching). Overall, results are consistent with the human developmental literature in demonstrating a tight interplay between emotional and social skills while highlighting the critical role of early experience (1–11, 27–30, 49).

Whereas the relationship between social and emotional functioning has received little attention in primate research, it has been widely demonstrated in human research (1–11, 27–30, 45, 47). Children more competent at regulating emotional responses to arousing events have more sociable temperaments, engage in more sustained social interactions, and are more likely to respond with sympathetic concern rather than personal distress (1–3, 6–11, 45–47). Our results, showing that juvenile bonobos with better ER skills (during self-distress as victims and in baseline) were more sociable, engaged in more frequent and more sustained social interactions, and showed more consolation, comfortably fits the same framework. Although our conclusions are based on a relatively small number of individuals, as is typical of great ape studies, larger sample sizes and future work incorporating physiological and experimental paradigms (such as skin conductance/heart rate in responses to emotionally arousing stimuli/distress in others) are bound to shed greater light on socio-emotional processes in nonhuman primates.

The effects of developmental background measured in this study highlight the influence of early deprivation on socio-emotional development. The lack of a stable caregiver is a stressor in human infant development (49), with institutionalized children showing increased anxiety and disrupted socio-emotional functioning (27–30, 49–51). In nonhuman primates, social deprivation studies have similarly demonstrated the role of species-typical maternal care in the development of cognitive and socio-emotional functioning (31–36). At the same time, however, our results demonstrate the striking resilience of these bonobo orphans. The fact that they were able at all to reconcile conflicts, console others (44), and engage in species-typical social interactions, such as play and grooming, suggests that they were managing reasonably well in their social world, likely buffered by the brief period of maternal care they had received. The substantial substitutive care received at the sanctuary must have helped, as also demonstrated by similar cognitive performance of these orphans compared with mother-reared juveniles (52) and the fact that many rehabilitated orphans at the sanctuary successfully raise their own offspring.

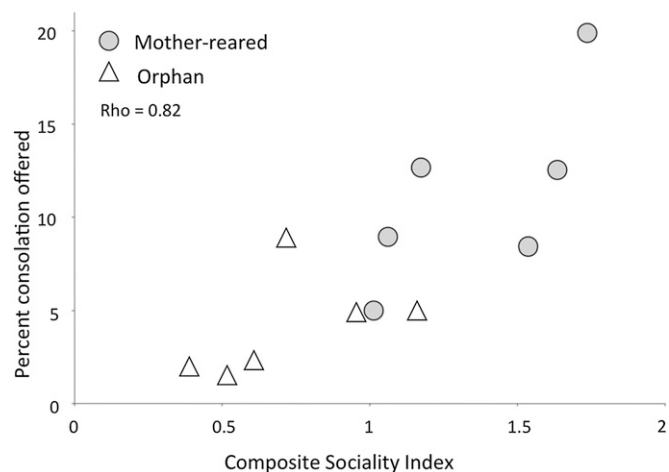


Fig. 3. Relationship between the offering of consolation to distressed parties and juvenile sociality (CSI). Each dot represents one individual ($n = 6$ orphan, $n = 6$ mother-reared subjects).

Lack of secure maternal support probably affects the behavior of orphans. Social conflicts can be risky, with renewed aggression potentially igniting larger disturbances. It may therefore be the orphans' best strategy to avoid tense scenes, either by remaining distant from the core group or fleeing at the sight of trouble. Their avoidant behavior was not necessarily maladaptive, therefore. However, it is the mother-reared juveniles that showed the full spectrum of social skills and socio-emotional responses typical of bonobos (16, 40, 44). They showed a tight interconnection between the regulation of their own emotions, their reaction to the emotions of others, and how they navigated their social world. We envision that continuity in this domain is not limited to the Hominoids but represents a more general primate, perhaps even mammalian pattern.

Methods

Study Site and Subjects. Observations were conducted at the Lola ya Bonobo Sanctuary, Kinshasa, Democratic Republic of the Congo. Most individuals arrived to the sanctuary as wild-caught orphans, rescued from the illegal bush-meat/pet trades as juveniles and subsequently rehabilitated. Some offspring were born and mother-reared at the Sanctuary (*SI Text* and *Table S1*). We observed group 1 ($n = 22$ individuals) and group 2 ($n = 20$ individuals) (*SI Text* and *Table S1*). This study was approved by Les Amis des Bonobos du Congo and complied with all requirements for conducting research in Democratic Republic of the Congo and with Emory University's Institutional Animal Care and Use Committee guidelines.

Data Collection. PD periods. From May to August 2012, observations were conducted by Z.C. and an assistant throughout the day (205 and 187 observation hours for group 1 and group 2, respectively). We conducted all-occurrence observations of agonistic interactions (*SI Text*), recording the identities of the initial recipient of the aggression (the "victim"), as well as the aggressor, and the identities of all visible bystanders. Because we were interested in responses to distress, we also recorded instances of spontaneous tantrums involving a single individual, in which there was no clear opponent (*SI Text*). For postconflict and tantrum events (PD periods), we recorded bystander proximity, context (feed/nonfeed), and conflict intensity (low, medium, and high).

Results from our previous study (44), conducted on the same subjects 1 y earlier, showed that consolation mostly occurred in the first few postconflict minutes (70.7% within the first 2 min, 84.6% within 5 min), hence we reduced the sampling time to 5 min. PD focals were filmed using a Canon Vixia HF200 HD Camcorder.

In the PD periods, (i) we recorded all instances of affiliative contacts between the focal and bystanders or the original opponent, including embrace, socio-sexual contact, touch, grooming, contact sit, play, hold, pat, and inspect (*SI Text*). We recorded the initiator of each interaction (the individual starting the contact). (ii) We coded the immediate responses, within 10 s, of all bystanders within 3 m of the onset of the PD period. The response of each proximate bystander was coded as positive, negative, neutral, or agonistic (*SI Text*). Receipt of positive affiliative contact from opponents and bystanders was also recorded. (iii) We coded the following victim responses during the PD period: duration of screaming bout(s); whether the focal recommenced spontaneously, screaming within the PD period in the absence of renewed aggression or provocation, following a pause of 30 s or more; and recovery time, as measured by the latency to cease showing any unprovoked anxiety response behaviors (i.e., teeth baring, self-embrace, whimpering; *SI Text*) taken from the last occurrence of one of these behaviors.

Juvenile social competence focals. We collected 15-min focal samples on the 12 juveniles ($n = 6$ mother-reared, $n = 6$ orphans; *Table S2*) during daily observation hours [501 focals, balanced across individuals: mean (\pm SD) 42 ± 4 focals per individual]. We continuously recorded all affiliative interactions involving body contact (i.e., play, groom, sexual contact, touch, contact sit, peering, embrace; *SI Text*), as well as aggressive interactions involving the focal. The onset and termination of play and grooming bouts were recorded to provide information about the frequency and duration of the interaction. We collected data on self-directed behaviors by recording rates of self-scratching per minute. We excluded all mother-offspring interactions from the database.

Affinity scans. Instantaneous scan samples ($n = 789$ in group 1, $n = 785$ in group 2) of all visible group members were conducted throughout the day (at fixed 10-min intervals), in which the identities of all individuals engaged

in affiliative state behaviors (i.e., groom, contact sit, sit within arms reach, play, sexual contact) were recorded.

Interobserver reliability. Cohen's κ coefficient was used to check for interobserver reliability for live and video coding. For live observations, reliability between the two observers was conducted at the beginning, middle, and end of the study period, obtaining an average value of Cohen's κ value of 0.89 (range, 0.84–0.93, $n = 5$ measures), rated as excellent. Forty PD videos (~10% of the total) were randomly selected and coded by an independent coder familiar with the ethogram, obtaining an excellent reliability rating (0.84; range, 0.56–1, $n = 9$ measures).

Data Analyses. Responses to other-distress. Consolation. After our demonstration of consolation using the postconflict-matched control method (15, 44), we here define consolation as the spontaneous offering of contact affiliation by a bystander toward a victim during the PD period. Contact directed by the victim itself toward the bystander was classed separately. We calculated the mean percentage of offered consolation per bystander as the number of PD periods in which they offered consolation divided by the number of PD periods witnessed. Using the same method, we calculated the probability of receiving affiliative contact from the victim. In both cases, we coded the first affiliative contact occurring in the first observed direction to ensure each PD period was counted only once per dyad.

PRI. To capture the negative and positive responses of bystanders, we examined the immediate responses (within 10 s) of all bystanders within 3 meters at the onset of the PD period. Focusing on positive and negative responses (i.e., excluding neutral responses), we created a PRI per individual, calculated as $PRI = (P - N)/(P + N)$, where P = number of PD periods in which the proximate bystander showed a positive immediate response, and N = PD periods in which this proximate bystander showed a negative response.

Responses to self-distress during PD periods: ER. We examined how mother-reared and orphan (each $n = 6$) juveniles responded as victims by comparing the following with nonparametric tests: mean duration of victim scream; mean latency to cease showing anxiety-related behaviors; and proportion of PD periods in which juveniles recommenced unprovoked screaming, in the absence of renewed aggression or provocation. To control for consolation, we separately examined these measures in the presence or absence of consolation. Having shown that the effects occurred in the same direction for both consolation and nonconsolation events (*SI Text*), we pooled the data for the main analyses. To investigate the relationship between ER and responses to distress as the victim and as the bystander, we conducted Spearman rank correlations on the probability of consolation as a bystander and the latency to return to relaxed behavior as a victim.

Juvenile social competence. We extracted four behavioral measures from the sociality focals and affinity scans thought to relate to social competence (and to interrelate to ER) in children: (i) mean length of each play episode, a putative marker of attention for sustained social interaction/attention (2); (ii) rate of initiated play episodes; a new episode began if play had ceased for more than 10 s [well-regulating children are bolder and engage in more social interactions (45)]; (iii) mean amount of play in seconds per hour; and (iv) mean number of closely bonded partners per juvenile, based on dyadic scores in the affinity scans within the upper range above the group median, excluding relations with their own mother. During the social competence focals, we also collected data on the mean rate of self-scratching per minute, a behavioral index of anxiety in primates (13, 14), which we used as a marker of baseline ER.

Composite sociality index. Adapted from ref. 46, we constructed a CSI to quantify the degree of sociality of each juvenile, representing overall social competence. We used a combination of four intercorrelated behavioral measures, extracted from the sociality focals and the affinity scans. The CSI indicated the degree to which each juvenile deviated from the population in their degree of sociality. The measures were (i) mean rate of initiated play per hour, (ii) mean amount of play in seconds per observation hour, (iii) proportion of focal observations in which the individual engaged in at least one affiliative interaction (*SI Text*), and (iv) individual affiliative tendencies, based on mean dyadic affiliation scores taken from the affinity scans. Dyadic affiliation scores were a combined measure of five affiliative behaviors occurring per dyad, divided by the scans in which both individuals were present. These were averaged across a subject's dyadic affiliative scores to calculate mean individual affiliative tendency. For mother-reared juveniles, interactions with their own mothers were excluded from analyses.

To construct the CSI, we verified whether the four measures were correlated. Having shown significant correlations between all measures (*Table S3*), we combined them into a single composite measure using (46): $\sum \frac{X_i}{m_i} / 4$, where X_i is the mean value per juvenile for each of the four measures, and m_i is the median value for the given affiliative measure. The sum of each affiliative value per juvenile, divided by the group median, was divided by

the number of behavioral measures in the analysis (i.e., 4). Higher CSI values represent greater sociality.

To investigate the relationship between sociality and responses to distress as the victim and as the bystander, we conducted Spearman rank correlations on the probability of consolation as a bystander and the CSI.

Determinants of consolation. GLMMs were applied with a binomial error structure and logit link function to examine the social determinants of juvenile consolation (lmer function, R package lme4). Social factors relating to the victim and bystander were examined, including sex (male/female), age (in years), rearing (mother-reared/orphan), bystander CSI, and bystander–victim dyadic affiliation score (see above). The binomial dependent variable was the occurrence of consolation, for each bystander present per PD event. We controlled for repeated sampling and individual variation by including six random effects: the identities of victim, aggressor, and bystander; the group in which they lived; the PD event, and the PD type (postconflict or tantrum). We found no strong collinearity among predictor variables and so computed all possible models using different combinations of predictor variables. The best model

was selected using the AIC, with the model with the lowest AIC value being the best to predict values of the dependent variable in a new data set. We compared the best model with the respective null model, which only contained random effects.

ACKNOWLEDGMENTS. We thank Pitshou Nsele Kayanga for assistance in data collection; Claudine André, Fanny Mehl, Dominique Morel, Valéry Dhanani, and Pierrrot Mbonzo and the Ministries of Research and Environment in the Democratic Republic of the Congo for their support (permit no. MIN.RS/SG/004/2009); the Lola ya Bonobo staff, particularly Stany Mokando and Jean-Claude Nzumbi; Brian Hare for support and comments, Malini Suchak for comments, and Philippe Rochat and Kim Bard for helpful discussions about social development; Tim Eppley for practical assistance; Emilie Genty and Gideon Malitskie for coding; Noah Snyder-Mackler for statistical assistance; and Takeshi Furuichi and Carolyn Zahn-Waxler for comments on previous versions of the manuscript. This work was financially supported by the Living Links Center of the Yerkes National Primate Research Center and Emory University's College of Arts and Sciences.

- Eisenberg N, Fabes RA (2005) Emotion regulation and children's socio-emotional competence. *Child Psychology: A Handbook of Contemporary Issues*, eds Balter L, Tamis-LeMonda CS (Psychology Press, New York), pp 357–384.
- Gross JJ, Thompson RA (2007) Emotion regulation: Conceptual foundations. *Handbook of Emotion Regulation*, ed Gross JJ (Guildford Press, New York), pp 3–24.
- Eisenberg N (2002) The socialisation of socio-emotional competence. *Improving Competence Across the Lifespan*, eds Pushkar D, Bukowski WM, Schwartzman AE, Stack DM, White DR (Kluwer Academic, New York), pp 59–78.
- Zahn-Waxler C, Hollenbeck B, Radke-Yarrow M (1985) The origins of empathy and altruism. *Advances in Animal Welfare Science* (Springer, New York), pp 21–41.
- Zahn-Waxler C, Robinson JL, Emde RN (1992) The development of empathy in twins. *Dev Psychol* 28(6):1038–1047.
- Eisenberg N, Spinrad TL, Sadovsky A (2006) Empathy-related responding in children. *Handbook of Moral Development*, eds Killen M, Smetana JG (Lawrence Erlbaum, Mahwah, NJ), pp 517–549.
- Rothbart MK, Ahadi SA, Hershey KL (1994) Temperament and social behavior in childhood. *Merrill-Palmer Q* 40(1):21–39.
- Eisenberg N, et al. (1996) The relations of children's dispositional empathy-related responding to their emotionality, regulation, and social functioning. *Dev Psychol* 32(2):195–209.
- Murphy BC, Shepard SA, Eisenberg N, Fabes RA, Guthrie IK (1999) Contemporaneous and longitudinal relations of dispositional sympathy to emotionality, regulation, and social functioning. *J Early Adolesc* 19(1):66–97.
- Davidov M, Zahn-Waxler C, Roth-Hanania R, Knafo A (2013) Concern for others in the first year of life: Theory, evidence, and avenues for research. *Child Dev Perspect* 7(2):126–131.
- Spinrad TL, et al. (2006) Relation of emotion-related regulation to children's social competence: A longitudinal study. *Emotion* 6(3):498–510.
- de Waal FBM (2008) Putting the altruism back into altruism: The evolution of empathy. *Annu Rev Psychol* 59:279–300.
- Fraser ON, Stahl D, Aureli F (2008) Stress reduction through consolation in chimpanzees. *Proc Natl Acad Sci USA* 105(25):8557–8562.
- Romero T, Castellanos MA, de Waal FBM (2010) Consolation as possible expression of sympathetic concern among chimpanzees. *Proc Natl Acad Sci USA* 107(27):12110–12115.
- de Waal FBM, Yoshihara D (1983) Reconciliation and redirected affection in rhesus monkeys. *Behaviour* 85(3/4):224–241.
- Palagi E, Paoli T, Tarli SB (2004) Reconciliation and consolation in captive bonobos (*Pan paniscus*). *Am J Primatol* 62(1):15–30.
- Roth-Hanania R, Davidov M, Zahn-Waxler C (2011) Empathy development from 8 to 16 months: Early signs of concern for others. *Infant Behav Dev* 34(3):447–458.
- Ungerer JA, et al. (1990) The early development of empathy: Self-regulation and individual differences in the first year. *Motiv Emot* 14(2):93–106.
- Parr LA (2001) Cognitive and physiological markers of emotional awareness in chimpanzees (*Pan troglodytes*). *Anim Cogn* 4:223–229.
- Nakayama K, Goto S, Kuraoka K, Nakamura K (2005) Decrease in nasal temperature of rhesus monkeys (*Macaca mulatta*) in negative emotional state. *Physiol Behav* 84(5):783–790.
- Stewart M, Stafford KJ, Dowling SK, Schaefer AL, Webster JR (2008) Eye temperature and heart rate variability of calves disbudded with or without local anaesthetic. *Physiol Behav* 93(4-5):789–797.
- Wascher CA, Scheiber IB, Kotschal K (2008) Heart rate modulation in bystanding geese watching social and non-social events. *Proc Biol Sci* 275(1643):1653–1659.
- Aureli F, Preston SD, de Waal FBM (1999) Heart rate responses to social interactions in free-moving rhesus macaques (*Macaca mulatta*): A pilot study. *J Comp Psychol* 113(1):59–65.
- Evans TA, Beran MJ (2007) Chimpanzees use self-distraction to cope with impulsivity. *Biol Lett* 3(6):599–602.
- Anderson JR, Kuroshima H, Fujita K (2010) Delay of gratification in capuchin monkeys (*Cebus apella*) and squirrel monkeys (*Saimiri sciureus*). *J Comp Psychol* 124(2):205–210.
- Evans TA, Beran MJ (2007) Delay of gratification and delay maintenance by rhesus macaques (*Macaca mulatta*). *J Gen Psychol* 134(2):199–216.
- Beckett C, et al. (2006) Do the effects of early severe deprivation on cognition persist into early adolescence? Findings from the English and Romanian adoptees study. *Child Dev* 77(3):696–711.
- De Bellis MD (2005) The psychobiology of neglect. *Child Maltreat* 10(2):150–172.
- Tottenham N, et al. (2010) Prolonged institutional rearing is associated with abnormally large amygdala volume and difficulties in emotion regulation. *Dev Sci* 13(1):46–61.
- Hodges J, Tizard B (1989) IQ and behavioural adjustment of ex-institutional adolescents. *J Child Psychol Psychiatry* 30(1):53–75.
- Sánchez MM, Ladd CO, Plotsky PM (2001) Early adverse experience as a developmental risk factor for later psychopathology: Evidence from rodent and primate models. *Dev Psychopathol* 13(3):419–449.
- Davenport RK (1973) Long-term cognitive deficits in chimpanzees associated with early impoverished rearing. *Dev Psychol* 9(3):343–347.
- van Ijzendoorn MH, Bard KA, Bakermans-Kranenburg MJ, Ivan K (2009) Enhancement of attachment and cognitive development of young nursery-reared chimpanzees in responsive versus standard care. *Dev Psychobiol* 51(2):173–185.
- Kempes MM, Gullickx MM, van Daalen HJ, Louwerse AL, Sterck EH (2008) Social competence is reduced in socially deprived rhesus monkeys (*Macaca mulatta*). *J Comp Psychol* 122(1):62–67.
- Harlow HF (1965) Total social isolation: Effects on macaque monkey behavior. *Science* 148(3670):666.
- Kempes M, Den Heijer E, Korteweg L, Louwerse A, Sterck E (2009) Socially deprived rhesus macaques fail to reconcile: Do they not attempt or not accept reconciliation? *Anim Behav* 78(2):271–277.
- Spijkerman RP, van Hooff JA, Dienes H, Jens W (1997) Differences in subadult behaviors of chimpanzees living in peer groups and in a family group. *Int J Primatol* 18:439–454.
- Sackett GP, Ruppenthal GC, Elias K (2006) *Nursery Rearing of Nonhuman Primates in the 21st Century* (Springer, New York).
- Prüfer K, et al. (2012) The bonobo genome compared with the chimpanzee and human genomes. *Nature* 486(7404):527–531.
- Furuichi T (2011) Female contributions to the peaceful nature of bonobo society. *Evol Anthropol* 20(4):131–142.
- de Waal FBM, Lanting F (1997) *Bonobo. The Forgotten Ape* (Univ California Press, Berkeley, CA).
- Rilling JK, et al. (2012) Differences between chimpanzees and bonobos in neural systems supporting social cognition. *Soc Cogn Affect Neurosci* 7(4):369–379.
- Preston SD, de Waal FBM (2002) Empathy: Its ultimate and proximate bases. *Behav Brain Sci* 25(1):1–20, discussion 20–71.
- Clay Z, de Waal FBM (2013) Bonobos respond to distress in others: Consolation across the age spectrum. *PLoS ONE* 8(1):e55206.
- Kagan J, Snidman NC (2004) *The Long Shadow of Temperament* (Belknap, Cambridge, MA).
- Silk JB, Alberts SC, Altmann J (2003) Social bonds of female baboons enhance infant survival. *Science* 302(5648):1231–1234.
- Light SN, et al. (2009) Empathy predicts dynamic change in prefrontal brain activity during positive emotion in children. *Child Dev* 80(4):1210–1231.
- de Vignemont F, Singer T (2006) The empathic brain: How, when and why? *Trends Cogn Sci* 10(10):435–441.
- Nelson CA (2000) *The Effects of Early Adversity on Neurobehavioral Development* (Lawrence Erlbaum, Mahwah, NJ).
- Ellis BH, Fisher PA, Zaharie S (2004) Predictors of disruptive behavior, developmental delays, anxiety, and affective symptomatology among institutionally reared romanian children. *J Am Acad Child Adolesc Psychiatry* 43(10):1283–1292.
- Zahn-Waxler C, Cole PM, Welsh JD, Fox NA (1995) Psychophysiological correlates of empathy and prosocial behaviors in preschool children with behavior problems. *Dev Psychopathol* 7(1):27–48.
- Wobber V, Hare B (2011) Psychological health of orphan bonobos and chimpanzees in African sanctuaries. *PLoS ONE* 6(6):e17147.