



Puberty initiates a unique stage of social learning and development prior to adulthood: Insights from studies of adolescence in wild chimpanzees

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ARTICLE INFO

Keywords:

Puberty
Adolescence
Pan troglodytes
Learning
Brain development
Social motivation

ABSTRACT

In humans, puberty initiates a period of rapid growth, change, and formative neurobehavioral development. Brain and behavior changes during this maturational window contribute to opportunities for social learning. Here we provide new insights into adolescence as a unique period of social learning and development by describing field studies of our closest living relatives, chimpanzees. Like humans, chimpanzees have a multiyear juvenile life stage between weaning and puberty onset followed by a multiyear *adolescent* life stage after pubertal onset but prior to socially-recognized adulthood. As they develop increasing autonomy from caregivers, adolescent chimpanzees explore and develop many different types of social relationships with a wide range of individuals in a highly flexible social environment. We describe how adolescent social motivations and experiences differ from those of juveniles and adults and expose adolescents to high levels of uncertainty, risk, and vulnerability, as well as opportunities for adaptive social learning. We discuss how these adolescent learning experiences may be shaped by early life and in turn shape varied adult social outcomes. We outline how future chimpanzee field research can contribute in new ways to a more integrative interdisciplinary understanding of adolescence as a developmental window of adaptive social learning and resilience.

1. Introduction

In humans, the onset of puberty begins a formative period of learning and social identity development (Dahl et al., 2018; Crone and Fuligni, 2020). Neurobehavioral changes contribute to increased proclivities for social exploration, sensation-seeking, and sensitivity to social value feedback (Ladouceur et al., 2019; Somerville, 2013; Foulkes and Blakemore, 2016; Rodman et al., 2017). These maturational changes tend to promote adaptive trial-and-error learning in a variety of ways. These include learning about the self and others, about ways to gain social value (e.g. to matter, to contribute), and about forming new kinds of social relationships/learning processes that are occurring as young adolescents explore and seek to navigate increasingly complex and uncertain social contexts (van den Bos et al., 2011; Foulkes and Blakemore, 2016; Pfeifer and Berkman, 2018; Fuligni, 2019; Westhoff et al., 2021; Hofmans and van den Bos, 2022). Importantly, this dynamic period of

social learning, development, and relationship formation is often an inflection point when young lives pivot along new trajectories in ways that can have long-term negative impacts. These include mental health problems, risk-taking and reckless behavior, substance abuse, and aggression. Yet, equally important, is understanding how this formative period of learning also creates a window of *opportunity*. Adolescence can be a critical time to support healthy, adaptive learning, resilience, and positive social development (Dahl et al., 2018; Orben et al., 2020; Duell et al., 2022; Fuligni and Galván, 2022; Karan et al., 2022).

Developmental research focusing on other species can provide new insights into how neurobehavioral changes associated with puberty appear to create a unique developmental window for adaptive learning. Research from rodents has provided fundamental understanding of how hormones involved in puberty are associated with specific brain and behavioral changes (Delevich et al., 2021). When it comes to understanding how more complex social motivational and behavioral

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proclivities change in relation to puberty, we may be able to gain novel insights by studying the natural behavior of species who like humans undergo an extended *adolescent* period of flexible social learning after puberty onset and before achieving socially-recognized adulthood. In chimpanzees (*Pan troglodytes*) this adolescent phase lasts many years and follows a multiyear post-weaning, pre-pubescent (juvenile) period (Fig. 1). Adolescent chimpanzees develop in large, dynamic social groups where individuals form many different types of social relationships with many different types of individuals (Goodall, 1986; Nishida, 2011). Beginning in adolescence, individual chimpanzees can spend long periods of time alone or with select companions other than family members. Their social relationships with individuals including parents, siblings, peers, and adult group members take on new forms during this period. For example, during adolescence, chimpanzees gain independence from their mothers (e.g. Pusey, 1983, 1990; Reddy and Sandel, 2020), are able to act as caregivers toward younger siblings (Hobaiter, 2014; Reddy and Mitani, 2019), seek the company of same-sex adults who can act as “mentors” (Nishida, 2011; Sandel et al., 2020), and begin to contribute reciprocally within dyadic friendships that form the basis for sexual reproduction and cooperative activities in adult life (Langergraber et al., 2013; Mitani, 2009; Mitani et al., 2000; Enigk et al., 2020; Reddy and Mitani, 2020; Samuni et al., 2020a, 2020b; Sandel et al., 2020; Reddy et al., 2021).

Chimpanzees, along with their sister species, the bonobo (*Pan paniscus*), are our closest living relatives. Our last common ancestor with both species is estimated to have lived between 5 and 7 million years ago—much more recently than our last common ancestor with frequent model species such as rhesus macaques (*Macaca mulatta*, 23 million years ago), laboratory rats (*Rattus norvegicus*, 65 million years ago) and laboratory mice (*Mus musculus*, 65 million years ago) (Glazko and Nei, 2003; Kumar et al., 2005) (Fig. 1). Because of our close evolutionary

relationship with chimpanzees and bonobos, we share many neurobiological, physiological, and social features. These include a prolonged adolescent period that occurs in a highly dynamic social world (Fig. 1).

Chimpanzees and bonobos are both endangered in the wild but bonobos are much rarer and found only in Democratic Republic of Congo. Due to chimpanzees’ relatively higher population numbers and wider, more politically stable geographic range, there is a larger body of research that tracks known individual chimpanzees compared to bonobos throughout development (Box 1). There are ten active wild chimpanzee research sites and two active wild bonobo research sites where animals have been continuously monitored for more than ten years, with the first ones beginning in 1960 (chimpanzees) and 1973 (bonobos) respectively (Hohmann and Fruth, 2003; Furuichi et al., 2012; Surbeck et al., 2017; McGrew et al., 2017; Thompson et al., 2020, Wilson et al., 2020). Due to the larger body of longitudinal research available on chimpanzees compared to bonobos, we focus on chimpanzees in this synthesis, making comparisons to adolescent bonobos, who notably have been the subject of both early and recent field studies (e.g. Idani, 1991; Kano, 1992; Toda and Furuichi, 2022; Toda et al., 2022) in a few key sections. Although we do not focus on bonobos here, studying bonobo adolescence as well as chimpanzee adolescence is equally critical for understanding our own species’ patterns. Importantly, chimpanzees and bonobos, which are estimated to have diverged from each other approximately 1 million years ago, differ in behavior, psychology and physiology, including in ways that co-occur in humans (Won and Hey, 2005; Hare and Yamamoto, 2017).

Although adolescence is a distinct life stage in chimpanzees, it has not historically been the primary subject of field studies (with a few notable exceptions: Pusey, 1977, 1990; Hayaki, 1988; Goodall, 1986; Nishida, 1989, 2003, 2011; Kawanaka, 1993). Recently, however, there has been a rapidly emerging expansion in understanding adolescence as

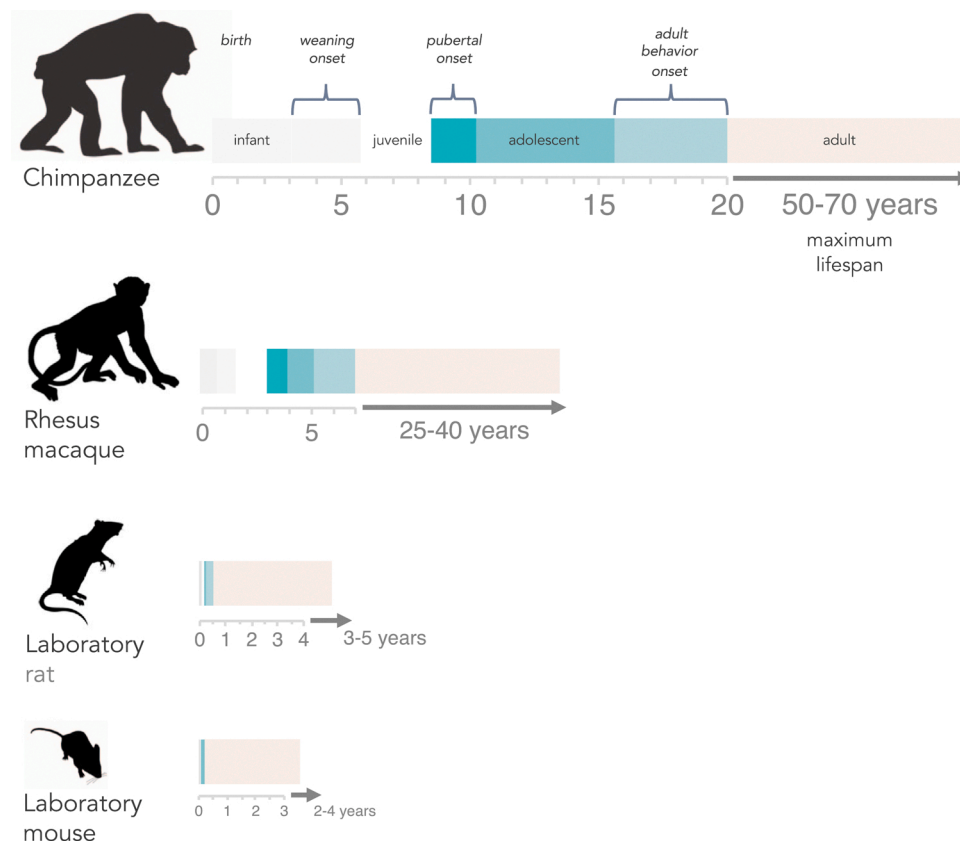


Fig. 1. Years allocated to adolescence in the life history of chimpanzees (*Pan troglodytes*) compared to three widely studied model species: Rhesus macaques (*Macaca mulatta*), laboratory rats (*Rattus norvegicus*), and laboratory mice (*Mus musculus*). Main references: Goodall (1986); Maestripietri and Hoffman (2012); Sengupta (2013); Brust et al. (2015).

Box 1
DATA PROVIDED BY LONGITUDINAL FIELD STUDIES OF CHIMPANZEES.



Above. Field observations of wild chimpanzees. Authors A.S. (left) and R.R. (right) observe known individual chimpanzees, Miles (left) and Jackson (right) who have been followed for decades by researchers at Ngogo in Kibale National Park, Uganda.

Above. Field observations of wild chimpanzees. Authors A.S. (left) and R.R. (right) observe known individual chimpanzees, Miles (left) and Jackson (right) who have been followed for decades by researchers at Ngogo in Kibale National Park, Uganda.

Our knowledge about chimpanzee social development comes from longitudinal field studies that can provide detailed information about known individuals from birth until death. Documentation of daily social interactions permits tracking of individuals' social relationships and social status throughout life. In addition to quantifying multiple aspects of social behavior, primatologists obtain measures of hormones and various biomarkers of growth and health from urine that we can pipette off of leaves and catch in plastic bags when individuals urinate from trees (e.g. Muller and Lipson, 2003) and feces which we collect from the ground. Such methods are constantly being improved to allow more fine-grained analyses of physiology (e.g. Behringer and Deschner, 2017). We also use video and laser photogrammetry to non-invasively measure body size and growth (e.g. Sandel et al., 2022) and can extract DNA from feces to determine genetic relationships between individuals (e.g. Vigilant et al., 2001). As a result of this close, consistent documentation on known individuals, we know the timing of individual developmental milestones such as the end of weaning, onset of puberty, first birth, and life events like maternal loss (e.g. Thompson, 2013; Samuni et al., 2020b; Stanton et al., 2020). We can further contextualize the environments in which individuals experience these events because we monitor community-level factors that fluctuate over time such as food availability (e.g. Potts et al., 2020), disease epidemics (e.g. Negrey et al., 2019, 2022), within-group political stability, and the threat of intergroup conflict (e.g. Sandel and Watts, 2021; Lemoine et al., 2020a, 2020b).

many chimpanzee field sites have collected longitudinal data on individuals from birth through adulthood, capturing adolescence as well as other hormonal and behavioral transitions during development (e.g., Walker et al., 2018; Sabbi et al., 2020; Enigk et al., 2020; Bründl et al., 2021). From these recent studies, including our own nearly decade-long study of adolescent male chimpanzees at Ngogo in Kibale National Park, Uganda (and recent field research on wild bonobos), we are advancing understanding of the key social features of this period (Reddy et al., 2021; Reddy and Mitani, 2019, 2020; Reddy and Sandel, 2020; Sandel et al., 2017, 2020, 2022; Reddy & Surbeck, unpublished data).

As noted above, adolescent chimpanzees begin to move autonomously apart from caregivers within a highly complex and flexible social world (Pusey, 1983, 1990; Reddy and Sandel, 2020; Reddy and Mitani, 2020; Sandel et al., 2020). How they behave in this flexible social world and how they are treated by others is distinct from juveniles and full adults (Hayaki, 1988; Pusey, 1990; Sandel et al., 2017, 2020; Enigk et al., 2020; Reddy and Mitani, 2020; Reddy and Sandel, 2020). These

years represent an extended window of social exploration and learning as well as vulnerability in this flexible social environment. In addition, events during adolescence are highly consequential for late life (e.g. Foerster et al., 2016), making it a potential inflection point for resilience against earlier life hardships.

In this paper we begin 1) by providing background on two features of chimpanzees that comparatively make them useful models for understanding social behavioral learning in human adolescence: a) their developmental life history patterns (Fig. 1, Fig. 2; Box 1) and b) the flexible, cooperative nature of their stable social relationships which take on new forms during adolescence (Fig. 3, Fig. 4, Fig. 5). Then (2) we describe in further detail the social motivational and behavioral changes that occur during chimpanzee adolescence, emphasizing how these adolescent-specific behavioral proclivities in chimpanzees can contribute to both adaptive learning and vulnerabilities. Next (3) we detail individual variation in social "outcomes" for adolescent chimpanzees and how, in parallel to humans, these outcomes may reflect

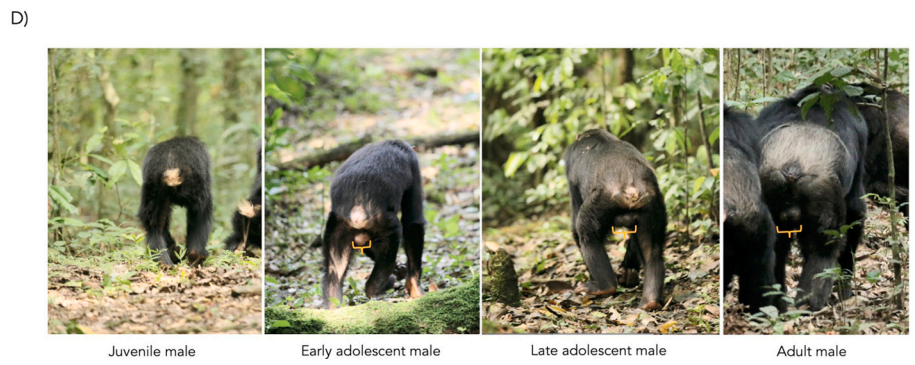
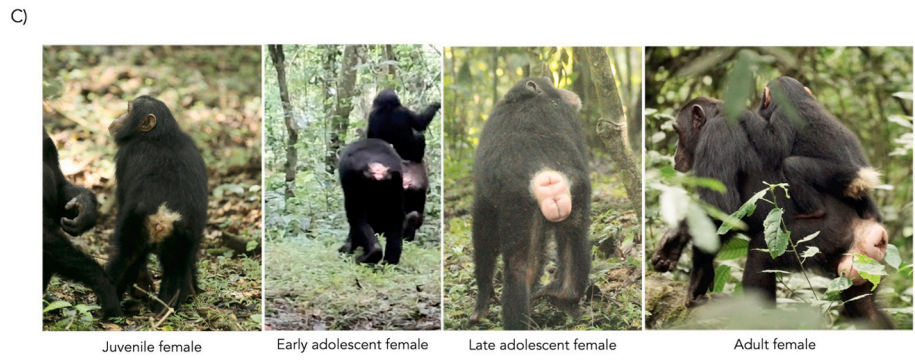
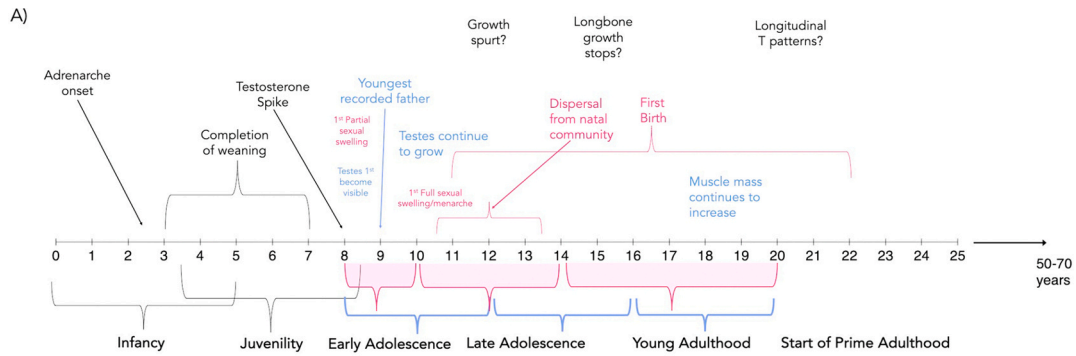


Fig. 2. A) A timeline of maturational markers from infancy to adulthood in chimpanzees. With one exception, data depicted in this figure come from wild chimpanzees and were accrued through continuous longitudinal observations and non-invasive physiological sampling of biomarkers in the urine and feces of known individuals (Box 1). Developmental patterns of urinary testosterone were measured in a large sample of zoo-living chimpanzees (Behringer et al., 2014). Markers shown in black text refer to milestones that apply to both sexes. Female-specific milestones are shown in pink and male-specific milestones are shown in blue. Visual depiction of B) increases in body size and the development of secondary sexual characteristics in C) females (sexual swelling enlargement) and D) males (testicular enlargement).
 Photos by Isabelle Clark, Kevin Lee, R.R., & A.S. Ngogo, Kibale National Park, Uganda, 2013–2022. References: Goodall (1986); Pusey (1990); Kawanaka (1993); Wallis (1997); Sugiyama (2004); Thompson et al. (2009); Nishida (2011); Langergraber et al. (2012); Thompson (2013); Behringer et al., 2014; Walker et al. (2018); Sabbi et al., 2020; Walker et al., 2018; Muller et al. (2020).

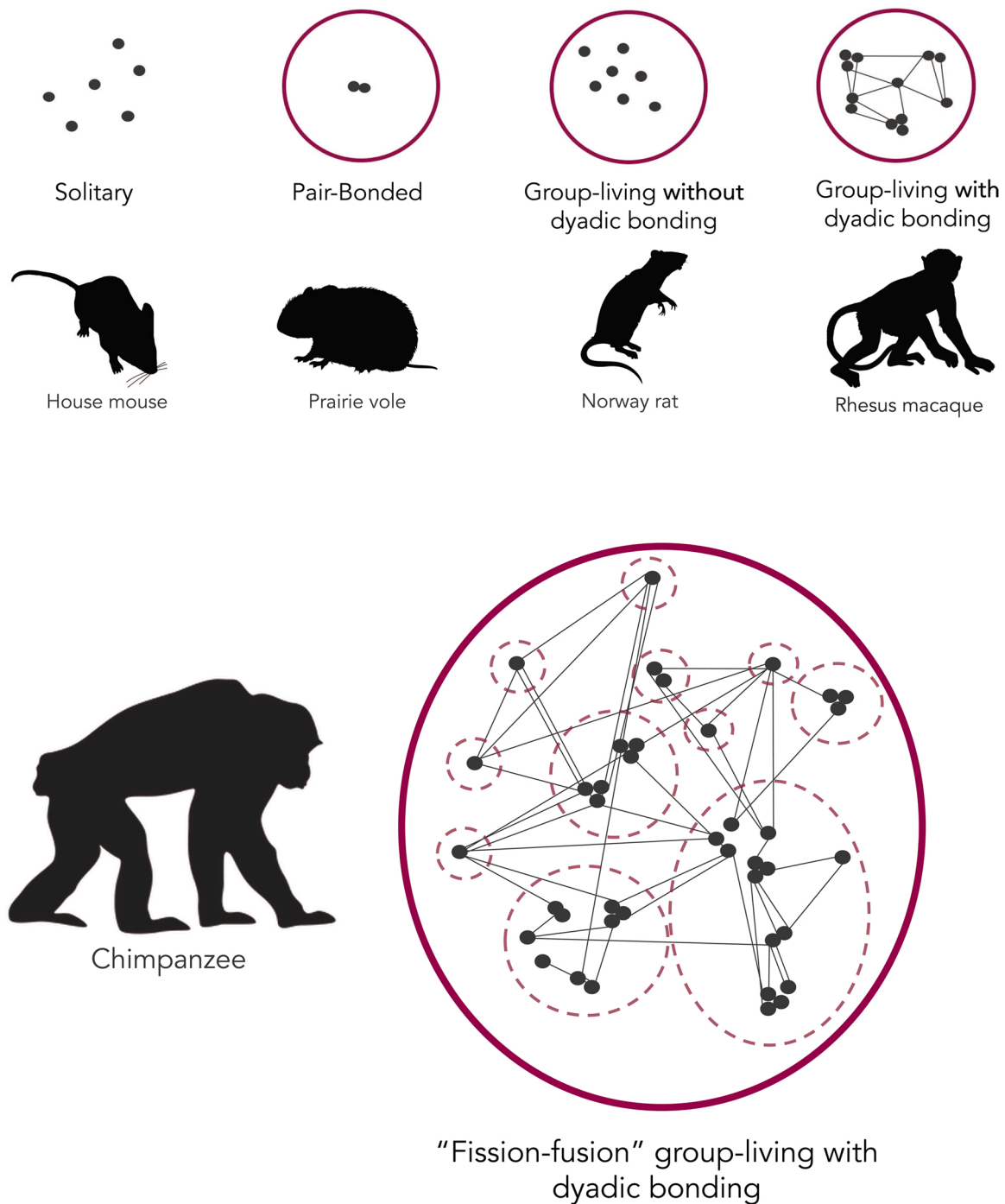


Fig. 3. Social organization in chimpanzees (*Pan troglodytes*) compared to (wild counterparts of) three widely studied model species: house mice (*Mus musculus*), prairie voles (*Microtus ochrogaster*), Norway rats (*Rattus norvegicus*) and rhesus macaques (*Macaca mulatta*).

inequalities in early life. Last, (4) we outline avenues for further studies on chimpanzee adolescence, that include understanding strategies for enhancing learning and improving resilience to early life adversity during the adolescent period in particular.

2. Why are wild chimpanzees useful models for understanding adolescence as an extended period of social learning in humans?

2.1. Patterns of development

Humans share some developmental patterns with other mammals, including rodent and macaque model species (Fig. 1). However,

chimpanzees, like humans, have a relatively extended juvenile period *and* extended adolescent period (Box 1; Fig. 1, Fig. 2). The juvenile period is distinct from infancy and begins, on average, around 5 years of age (Box 1; Fig. 2; Goodall, 1968, 1986; Pusey, 1983; Nishida, 2011; Thompson, 2013; Bründl et al., 2021). Juvenility is preceded by adrenarche, which occurs in late infancy (~2–3 years of age) and has been suggested to be associated with sex variation in aggressive behavior; Fig. 2; Sabbi et al. (2020), (2021). The beginning of the juvenile stage is marked primarily by the cessation of (a) nursing, (b) being carried by mothers during travel, and (c) sleeping together with mothers in a single night nest rather than constructing one's own beside mothers (Box 1; Fig. 2). Juveniles as well as older infants also engage more frequently

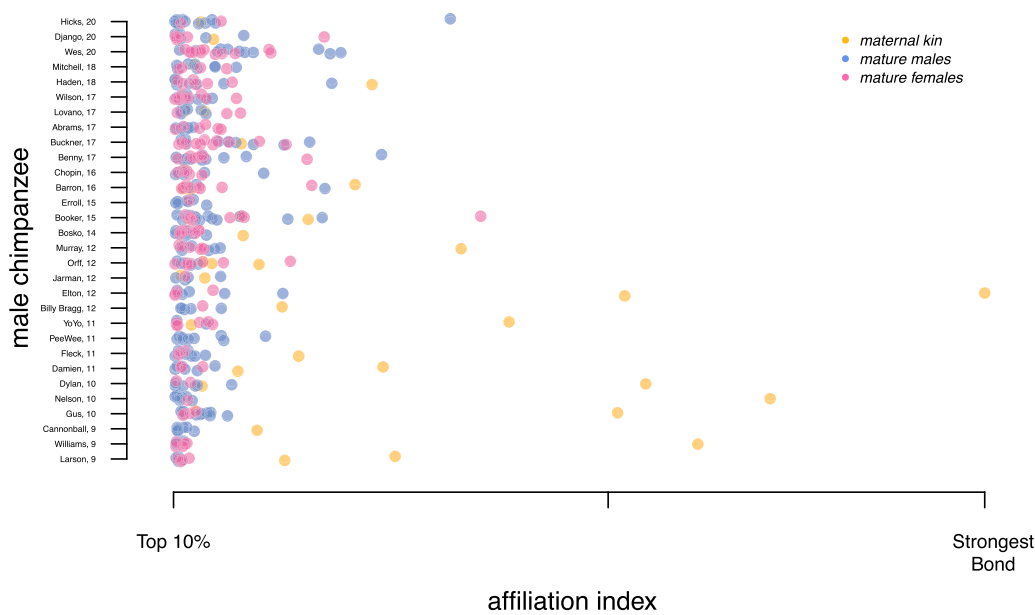


Fig. 4. Male chimpanzees form more strong bonds with non-family members as they pass from early adolescence to young adulthood ($n = 30$ males; 9 – 20 years old). Each data point indicates a social bond formed by the male on the y axis and another group member (maternal kin including mothers and siblings, non-kin mature males and non-kin mature females). All pairs shown ($n = 401$) are strongly bonded pairs, defined as pairs whose affiliation indices, a composite measure of bondedness comprising the frequencies of time spent grooming and in spatial proximity, fell in the top 10% of the distribution of affiliation indices of all possible pairs in the community. Pairs farthest from the origin along the x axis are the strongest of these strongly bonded pairs. Males are shown in ascending age order on the y axis, with the youngest male near the origin at age 9 years and the oldest at the top at age 20 years.

Reproduced from Reddy and Mitani (2020).



Fig. 5. A moment of social anxiety engendered by the features of fission-fusion group life: Adult male chimpanzee Richmond mounts and holds on to his brother Hutcherson when they hear calls of group members they have not yet seen this day gathering nearby. Richmond and Hutcherson must now decide whether to join or avoid this gathering.

Photo by Nathan Chesterman. Ngogo, Kibale National Park, 2014.

and widely in social interactions such as grooming, play and aggression with both siblings and non-family members (Box 1; Goodall, 1968, 1986; Pusey, 1983; Nishida, 2011; Sabbi et al., 2021).

Although juveniles may interact socially with many individuals, their mothers and dependent siblings are, by far, their primary social partners (Pusey, 1983; Goodall, 1986). Critically, most social interactions of juveniles occur in the presence of mothers because juveniles travel almost constantly with mothers during this period. And, if temporarily apart from mothers (or orphaned), juveniles typically remain in the company of other adults, who often show them tolerance, affection, and even care, especially when mothers are absent (Box 1; Pusey, 1983, 1990; Uehara and Nyundo, 1983; Goodall, 1986; Boesch et al., 2010; Pruetz, 2011; Hobaiter et al., 2014; Nakamura and Nishie, 2019; Reddy and Mitani, 2019). These patterns of social behavior change during adolescent development (Box 1; Pusey, 1983, 1990; Reddy and Mitani, 2020; Reddy and Sandel, 2020).

Adolescence is marked by the onset of puberty, including changes in hormones, growth and the appearance of secondary sexual characteristics (Fig. 2). The clearest indicators of puberty in wild chimpanzees are when the sexual skin becomes swollen, indicating the onset of reproductive cycling regulated by gonadal hormones, in females (Fig. 2), and the testes become visible in males (Hobson et al., 1976; Pusey, 1990). Based on these metrics, puberty begins between ages 8 and 10 years for both male and female chimpanzees in the wild (Takasaki, 1985; Nishida, 2003, 2011; Sugiyama, 2004; Goodall, 1986; Pusey, 1990; Thompson, 2013; Walker et al., 2018). This period of onset coincides with a testosterone spike for both male and female chimpanzees in captive populations, with this spike being relatively higher in males (Anestis, 2006; Behringer et al., 2014). In subsequent years, the testes and sexual swellings continue to enlarge into middle and late adolescence (Goodall, 1986, 1997; Thompson et al., 2009; Thompson, 2013; Fig. 2).

The start of adolescence is relatively straightforward, being marked by puberty onset. The end of adolescence, however, is more ambiguous. This is partly due to the fact that, as in humans, reaching adulthood is primarily a social distinction (Box 2). There is considerable individual, community, and population-level variation in when chimpanzees are considered adults. Adulthood for chimpanzees is rooted in individual competence and recognition by group members. It can include factors such as recruitment by other adults as coalition partners (e.g., Enigk et al., 2020), receiving pant-grunt greeting calls that indicate subservience from particular individuals (e.g., Bygott, 1974), being groomed reciprocally by particular individuals, being waited for, and being able to be a competent parent (including for males as adoptive caregivers: teenage adopters often do not see their charges survive for as long, Hobaiter et al., 2014) (Box 2; Fig. 1, Fig. 2; Goodall, 1986; Nishida, 1989, 2011; Kawanaka, 1993; Hansen, 2017; Sandel et al., 2017; Watts, 2018; Enigk et al., 2020; Sandel et al., 2020; Reddy and Mitani, 2020). In many chimpanzee communities, there is a distinct young adult period, ranging from ~ 16–21 years of age, when some but not all prime adult competencies are reached (Box 2; Fig. 1, Fig. 2; Goodall, 1986; Nishida, 1989; Kawanaka, 1993; Nishida, 2011; Hansen, 2017; Sandel et al., 2017, 2020; Reddy and Mitani, 2020; Reddy and Sandel, 2020; Reddy et al., 2021).

The onset of adolescence in chimpanzees is associated with a profound social re-orientation—away from maternal family relationships and toward new potential social partners and social activities that

Box 2 SOCIAL BEHAVIORS OF CHIMPANZEE DEVELOPMENTAL LIFE HISTORY STAGES.



Infant



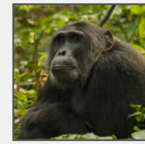
Juvenile



Early Adolescent



Young Adult



Prime Adult



Middle Age

Infancy (birth-5y)

- Carried by mother during travel.
- Sleep in same night nest as mother.
- Are in almost constant physical contact with mothers for 1st year of life.
- Mother and maternal siblings are primary social partners, but also engage in play and other forms of social touch with unrelated adults and older immature individuals, especially in later infancy and especially if they have a mother who is socially connected rather than peripheral herself.
- Typically do not survive for long following maternal loss.

Juvenility (5-8y)

- Travel constantly with mother (and almost never left alone) but are no longer carried by her.
- Make own night nest for sleeping, beside mothers' nest.
- Mother and maternal siblings are primary social partners, but also engage in play and other forms of social touch with unrelated peers and adults, especially if they have a mother who is socially connected rather than avoidant herself.
- Receive little aggression and often affectionate touch from unrelated adults.
- Often survive maternal loss with care from adult adoptive parent.

Early Adolescence

Females (8-10y)

- Travel and groom (touch) often with mother, but begin to separate from her without distress to explore other neighborhoods of the community.
- Follow and attempt to mate with adolescent and young adult males.
- Follow and groom peer or older females other than mother.

Males (8-12y)

- Gradually travel away from mother including spending nights away from her to follow adult males, though mother remains primary social partner.
- Unlike females show distress upon separating from mother (e.g. whimpering while looking back and forth between mother and group of adult males she chooses not to join).
- Become wary of adult males and show them extreme submission (e.g. repetitive high-arousal version of typical pant grunt greeting vocalization that is given by subordinate individuals to higher status individuals-including by juveniles to most adults-often accompanied by bowing). Adult males withdraw affectionate touch from adolescent males and this can also cause distress.



Old Age

Late Adolescence

Females (10-14y)

- Make visits to other communities alone, and usually disperse permanently.
- As immigrants, face extreme pressure to integrate and establish oneself socially as this "first impression" has lifelong consequences for status.
- Immigrant females receive extreme aggression from resident females and seek physical touch from old resident females often in the form of sociosexual behavior.
- Frequently join on boundary patrols.

Males (12-16y)

- Work to dominate females.
- Avoid dominance interactions with male peers.
- Receive a lot of aggression from and show extreme subordination toward adult males.
- Still spend considerable time with mother but she gradually stops being the primary social partner of most males.
- Provide one-sided grooming to elderly male "mentors," and older maternal brothers as they remain on the outskirts of adult male social life.
- Groom more reciprocally with male peers and females.
- Begin joining boundary patrols without caregiver present (individual variation).
- Heightened risk of death compared to other ages (from inter-group killings).

Young Adulthood

Females

- Give birth to their first infant, who is at high risk for infanticide as a newborn.
- Continue to establish oneself socially and receive more aggression from resident females than older females.
- Travel with more selective company or "alone" with just offspring.
- Reduce participation in boundary patrols (with considerable interindividual variation).

Males (16-20y)

- Dominate all females in group but not yet integrated into adult male hierarchy.
- All males groom (touch) their mother when they travel in the same subgroup as her, but only 1/3 have mother as primary social partner.
- Bonds with other group members have increased in strength, number, and equability.
- Can be competent adoptive parents for orphans (e.g. adoptees are more likely to survive to adulthood).
- Heightened risk of death compared to other ages (from inter-group killings, boundary patrols).

Prime Adulthood

Females

- Give birth to second infant and are fully socially established.

Males (21y+)

- "Make moves" to become high-ranking if interested in achieving high-rank status in the male hierarchy.
- Hold highest status in male hierarchy during these years.
- Reduced risk of death compared to late adolescents and young adults (from intergroup killing).

Photos: Kevin Lee & R.R., Ngogo, Kibale National Park, Uganda 2014 -2017.

contribute to learning relevant to achieving adult social success (Sandel et al., 2020; Reddy and Mitani, 2020; Fig. 4). For males, this reorientation occurs within their own social groups, while females typically emigrate to new social groups between 11 and 13 years of age, eventually settling in one permanently (Nishida, 1979; Pusey, 1979; Thompson, 2013). While adolescents are seeking connections with these

non-family social partners, those social partners are showing negative changes in their behaviors toward adolescents—no longer treating them with the tolerance, affection, and care given to juveniles (Box 2; Goodall, 1986; Pusey, 1990). That is, at the same developmental transition as adolescents appear motivated to socially explore and form new bonds, the potential new social partners are likely to exclude them, making

adolescents newly vulnerable to social rejection (Box 1). We describe the social features of the adolescent period in further detail in Section 3.

2.2. Social Relationships

The flexibility and complexity of chimpanzee social relationships, which take on a new form during adolescence, provide parallels to the complex social choices human adolescents encounter. Such choices are fundamental to the social learning challenges human adolescence face while they learn to navigate increasingly novel and complex social contexts. To help elucidate these human-chimpanzee parallels, we briefly provide some broader understanding of mammalian social organization. We provide examples of social organization systems of common model species in their wild forms, including house mice (*Mus musculus*), prairie voles (*Microtus ochrogaster*), Norway rats (*Rattus norvegicus*), and rhesus macaques before describing how the flexibility and complexity of chimpanzee social relationships—about which they begin to make autonomous choices in adolescence—more closely mirror those of humans (Fig. 3).

All mammals form close bonds with their mothers in infancy, on whom they entirely depend for sustenance (Hinde, 1979; Seyfarth and Cheney, 2012). Maternal-offspring bonds in mammals involve frequent, dependable affiliative touch (Harlow and Harlow, 1965; Hinde, 1979; Box 5). However, many mammals never again form such a bond with another adult after pubertal onset. Instead, they lead relatively solitary lives as adults, engaging only in affiliative touch with their dependent offspring and, with the exception of occasional mating, ignore, avoid, or aggress other conspecifics (e.g. Kondrakiewicz et al., 2019). This relatively solitary adult life is often considered to be the ancestral condition for all mammals (Shultz et al., 2011; Lukas and Clutton-Brock, 2013). It is the “condition” of wild house mouse for whom adult-adult affiliation is occasional; it occurs, for example, when females who are not pregnant or lactating nest together and huddle for warmth (Kondrakiewicz et al., 2019). Other mammals, such as prairie voles, form close, affiliative pair bonds after dispersing from caregivers (Lukas and Clutton-Brock, 2013; Madrid et al., 2020). These social pair bonds involve mating and parenting together, but bond partners engage in affiliative interactions only with their mates and offspring—their pair bond represents the entirety of their social “group,” and they often show hostility to anyone other than their partner or their offspring (Fig. 3). Other mammals live in large social groups where individuals behave affiliatively toward each other (e.g. play, grooming, predator vigilance and protection) yet do not form stable, differentiated, preferred social bonds with other adult members of their groups. Wild Norway rats are described to form such friendly groups that lack differentiated bonds (Schweinfurth, 2020; Kondrakiewicz et al., 2019; Schweinfurth, 2020) (Fig. 3). It is important to note that a lack of preferential dyadic-bonding-beyond-dependent-offspring does not indicate that animals have reduced emotional or social cognitive capabilities. For example, in experiments captive laboratory rats regularly cooperate with and help similarly aged group members. In one experiment rats gave up food rewards to free their distressed cage mates who were being soaked with water (Sato et al., 2015; Schweinfurth, 2020). Rather, species with the preceding forms of social organization simply differ from humans, who live in large, ever-expanding social groups and form many different types of differentiated social relationships with different individuals throughout life (Seyfarth and Cheney, 2012).

In contrast to rodent species, rhesus macaques and chimpanzees adopt a more human-like form of social organization. Specifically, they form large, relatively stable social groups comprising individuals of all ages and sexes. Throughout life they have differentiated dyadic bonds with multiple individuals within these groups (Fig. 3, Smuts et al., 1985; Goodall, 1986; Nishida, 2011; Maestriperi and Hoffman, 2012; Seyfarth and Cheney, 2012). Chimpanzees groups are called communities and range between 20 and 200 individuals. Males remain in the group they are born in for life while females emigrate and permanently settle in new

groups during adolescence (Nishida, 1968, 1979; Pusey, 1979; Goodall, 1986; Wood et al., 2017). Macaque groups, called troops, can range similarly in size (particularly in a provisioned population on Cayo Santiago in Puerto Rico) but males disperse while females remain in their natal groups (Maestriperi and Hoffman, 2012). Dyadic bonds in group-living rhesus macaques and chimpanzees, in contrast to pair-bonded, pair-living species like prairie voles, are not restricted to mating and parenting. In both macaques and chimpanzees, males and females mate regularly with multiple partners and mothers are typically sole caregivers of offspring. Dyadic bonds are formed between individuals of all sexes. They are defined by the relative frequency and reciprocity of affiliative behaviors including spatial proximity, touch (e.g. grooming), and reliable coalitionary support in aggressive conflicts (Goodall, 1986; Mitani, 2009; Nishida, 2011; Maestriperi and Hoffman, 2012; Seyfarth and Cheney, 2012; Samuni et al., 2020a, 2021). Through such aggressive coalitionary support, social bonds can elevate individuals’ dominance status (Silk et al., 2002; Seyfarth and Cheney, 2012).

Chimpanzees have more flexibility than macaques when it comes to forming these social relationships, and this flexibility emerges during adolescence. When we compare only *philopatric* individuals in each species—that is, the individuals who remain in the group of their birth for life—social relationships change profoundly for chimpanzees (males are philopatric) but less so for macaques (females are philopatric). This is because female macaques, like the majority of social mammals, form differential affiliative dyadic bonds primarily with their close genetic kin, particularly their mothers and their maternal sisters to whom they have been bonded since infancy and with whom they remain together for life (Maestriperi and Hoffman, 2012; Silk et al., 2002; Seyfarth and Cheney, 2012). Female macaques “inherit” their status directly from their mothers who support them consistently in aggressive conflicts. They consequently maintain social positions in line with their entire family’s (Holekamp and Smale, 1991; Silk et al., 2002).

Chimpanzee males, like macaque females, form a close bond with their mother and maternal siblings from birth (Pusey, 1983; Takahata, 1990; Langergraber et al., 2007; Mitani, 2009; Reddy and Sandel, 2020; Sandel et al., 2020). However, unlike female macaques, male chimpanzees regularly grow up to form their closest bonds with individuals who are *not* their close maternal kin (Mitani et al., 2000; Silk et al., 2002; Mitani, 2009; Langergraber et al., 2007; Seyfarth and Cheney, 2012; 2020; Bray and Gilby, 2020; Bray et al., 2021a). This change occurs in adolescence (Fig. 4), as becoming a socially and reproductively successful male chimpanzee requires forging and maintaining social relationships with family members and non-family members (Nishida, 1983; Langergraber et al., 2013; Bray et al., 2021b; Feldblum et al., 2021; Reddy et al., 2021). Importantly, male chimpanzees do not “inherit” familial rank status. Although infant and juvenile chimpanzees do gain increased social and nutritional resources from having a high-status mother, beginning in adolescence they must earn their social status independently from her (Pusey et al., 1997; Markham et al., 2015). It is possible, for example, for a female chimpanzee to have one son who becomes “alpha male” and another who never attains a high-rank position. To achieve high dominance rank, male chimpanzees must successfully form strong bonds and alliances with other males who may or may not include their maternal brothers. As noted above, earning this type of status is not the only route to social and reproductive success for male chimpanzees. Forming strong social bonds with males and females also leads to reproductive opportunities, independently of dominance rank (Nishida, 1983; Langergraber et al., 2013; Bray et al., 2021a; Feldblum et al., 2021). In addition to forming reciprocal social bonds with other adult non-kin, male chimpanzees engage in one-sided caregiving relationships with non-kin. Males regularly adopt young orphans, regardless of genetic kinship, especially if these vulnerable orphans lack adult maternal siblings to adopt them (Boesch et al., 2010; Hobaiter et al., 2014; Reddy and Mitani, 2019).

In essence, the formation of social bonds, particularly in adolescence,

by dispersing females as well as philopatric male chimpanzees (Wakefield, 2008, 2013; Langergraber et al., 2009, 2013; Lehmann and Boesch, 2009; Foerster et al., 2015; Samuni et al., 2018, 2020a, 2020b, 2021; Reddy and Mitani, 2020), are the basis of chimpanzee social organization. In addition to grooming, maintaining spatial proximity, and forming coalitions and alliances, bonded chimpanzees make efforts to keep track of each other during travel so that they can spend time together in the same subgroups, provide each other with comforting touch (e.g. embracing and holding hands), share meat, and sleep in night nests built near each other (Nishida, 1983; Mitani et al., 2000; Samuni et al., 2017; Reddy and Mitani, 2020; Sandel et al., 2020). Bonded individuals are also more likely to engage in a dangerous collective activity that has few parallels in nonhuman species: “war-like” patrols of territory borders where individuals may kill or be killed by chimpanzees from other communities (Mitani et al., 2000; Samuni et al., 2020a, 2021). Boundary patrols and lethal intergroup aggression facilitate chimpanzees maintaining their current territory and/or taking over land from other chimpanzee communities to acquire new food resources (e.g. Mitani et al., 2010). In lethal intergroup conflicts such as these, chimpanzees risk dying for each other (e.g. leaping in to cover the body of a friend who is being fatally beaten, Sandel and Watts, 2021).

The dyadic bonds chimpanzees form during their lives, and the memories they have of their bond partners can endure for decades (Mitani, 2009; Bray and Gilby, 2020; Lewis, 2022). Chimpanzee bonds endure longer than bonds in macaques or rodents because chimpanzees live longer. Chimpanzees have longer lifespans than macaques, often reaching their 50 s in the wild (Fig. 1; Wood et al., 2017). In addition, chimpanzees face lower mortality rates after infancy than do smaller-bodied animals who are more easily killed by predators as adults (e.g., Seyfarth and Cheney, 2012: in 50% of all pairs of wild female baboons who were part of a longitudinal study of dyadic social relationships in Moremi Game Reserve in Botswana, at least one individual had died after a 3-year-period). The duration of chimpanzee social relationships has relevance not only to aspects of social learning in humans, but also to the human scale of long-term memories, a core feature in the neurobiological development of emotional disorders (Pine et al., 2021).

In addition to flexibly choosing long-lasting bond partners and flexibly earning status, chimpanzee communities compared to rhesus macaque troops have an additional dimension of social flexibility and complexity. In contrast to macaque troops, whose members are almost always within view of each other and travel together as a single unit (and being alone often means getting eaten), chimpanzee communities are fission-fusion social groups (Nishida, 1968, 1979; Sugiyama, 1969; Aureli et al., 2008; Maestriperi and Hoffman, 2012; Fig. 3). In their fission-fusion communities, chimpanzee group members share a bounded territory (and between-group interactions are lethally hostile: Wilson et al., 2014) but can move separately within it. They travel alone or in ephemeral subgroups that vary in size and composition and change—fissioning or fusing with other individuals or subgroups—at any given moment (Nishida, 1968; Fig. 3). This means that chimpanzees, in contrast to rhesus macaques, can choose, moment-to-moment, to spend time alone or to seek and maintain social proximity with individuals or subgroups. Although chimpanzees know and recognize many individuals as members of their community, they are rarely all together at once. They can go hours, days, weeks, and even months without seeing certain group members (Nishida, 1968, 1979; Sugiyama, 1969). They can choose to spend a day or week in the company of a few close friends, take “alone time,” or go to visit their mother in their “childhood neighborhood” (which they do habitually when food is scarce: Murray et al., 2008, pers. obs.).

These dynamic social choices to separate and reunite appear to cause anxiety in chimpanzees (Fig. 5). Moments of reunion with community members are often tense, even if individuals are reuniting with someone after just a few hours apart (e.g. Sugiyama, 1969). Each reunion may involve a reassessment of the standing of social relationships. As a result,

when chimpanzees hear another individual approaching or a large gathering in the distance they may grimace, whimper, or hold onto other individuals (Fig. 5; Goodall, 1968). When these gatherings form, there is often chasing, screaming, and more reassuring touch, including kissing on the mouth and embracing (e.g. Goodall, 1968; Sandel and Reddy, 2021). These daily occurrences of choosing to join or avoid a potential social interaction are emotionally heightened regardless of what individuals ultimately choose to do. As in humans, there is tremendous variation in individuals’ proclivities to join or avoid socializing at all, and these proclivities shift with negative life experiences such as being badly beaten up by group members or losing a best friend.

Importantly, these individual social-motivational proclivities also change during adolescent development. It is in adolescence when chimpanzees start to make these flexible social choices autonomously, to join or avoid interacting with group members (Pusey, 1990; Reddy and Sandel, 2020). As mentioned in the last section, before adolescence, chimpanzees are almost never left alone (e.g., Nakamura and Nishie, 2019). As infants and juveniles, they are carried or follow their mother and socialize with whoever she socializes with or may occasionally travel with another adult (or permanent adoptive parent) who, often, will wait for them and ensure they follow (Box 1; Goodall, 1968; Pusey, 1983; Uehara and Nyundo, 1983; Pruett, 2011; Hobaiter et al., 2014; Reddy and Mitani, 2019; Bründl et al., 2021). Adolescent chimpanzees thus have newfound independence to explore within this flexible fission-fusion social system and to be faced with choices that may induce anxiety-like behavior (Fig. 5). Adolescent chimpanzees may also become witness to social events and activities that they have never seen in the past, simply because their mother did not join such events or activities (see Section 3).

Overall, adolescence is a key developmental phase when wild chimpanzees are learning how to form and maintain dyadic, affiliative, potentially lifelong and often reciprocal relationships that are crucial to adult social success. It appears that adolescence represents a formative stage of learning when chimpanzees begin to *prioritize* such dyadic relationships outside of their maternal families (Box 1; Fig. 4; Hayaki, 1988; Kawanaka, 1993; Foerster et al., 2016; Enigk et al., 2020; Reddy and Mitani, 2020; Sandel et al., 2020). In addition, adolescent chimpanzees begin to develop a wider range of prosocial behaviors and more complex social relationships in a manner that juveniles and infants do not (Fig. 6; Box 3). For example, an adolescent chimpanzee may begin to provide coalitionary support to his older brother and act as an adoptive caregiver to his younger one (e.g. Fig. 6; Reddy and Mitani, 2019; Enigk et al., 2020). We elaborate on these changes and the nature and variation in social relationships formed by adolescent chimpanzees of both sexes in the next section.

3. Social motivation and experiences in chimpanzee adolescence: A period of risk-taking, exploration and learning

Chimpanzee adolescence is characterized by a major behavioral social-reorientation. During adolescence, chimpanzees begin to “fledge.” They travel independently of their mothers who have provided them with reliable affection and protection in earlier life (Box 2-4; Goodall, 1968, 1986; Pusey, 1983, 1990; Reddy and Sandel, 2020). They begin to explore their wider community territory, spending time alone for the first time, and initiating social interactions with non-family members that have new dimensions. This independent social exploration also represents a key developmental stage for learning how to be a successful, socially connected adult chimpanzee; however, it exposes adolescents to numerous risks and vulnerabilities. Not only do adolescents leave maternal protection (e.g. Reddy et al., submitted), but they may engage for the first time in risky activities such as participating in territory boundary patrols where lethal aggression may occur (Box 3; e.g., Watts and Mitani, 2001; Langergraber et al., 2017). Adolescent chimpanzees also face new risks of social ostracization and rejection. Specifically, they encounter a withdrawal of the previously positive

Box 3**THE DEVELOPMENT OF PROSOCIAL BEHAVIORS DURING CHIMPANZEE ADOLESCENCE.**

During adolescence, humans begin to re-orient toward non-caregiver social partners and explore a broader range of social contexts than they did in earlier life (Nelson et al., 2016). The preceding behavioral proclivities create many opportunities to learn about prosocial behaviors and forming new types of social relationships. Such social learning experiences contribute to adolescents' developing sense of self and social identity (Crone and Fuligni, 2020). In humans, prosocial actions such as helping or sharing are highly influenced by forces such as reputational prestige and existence of third-party enforced social norms that shape status and value in a particular society (e.g. Henrich and Muthukrishna, 2021), and may be distinct from cooperative behavior in chimpanzees. For example, both children and zoo or sanctuary-living captive chimpanzees demonstrate proclivities to help others at early ages in similar experimental contexts (Warneken and Tomasello, 2006; Greenberg et al., 2010; Yamamoto et al., 2012). However, by five years of age children's positive emotions when helping others appear enhanced by an audience, a factor that does not affect the positive emotions of 2-year-old children in the same experiment (Hepach et al., 2022). Another experimental study showed that 5-year-old children but not chimpanzees (who ranged in age) were more likely to share and less likely to steal from others when a peer watched them compared to when unobserved, suggesting that reputational concerns influenced children's but not chimpanzees' prosocial proclivities (Engelmann et al., 2012). These varied motivations for prosociality in our species reflect our heightened interdependence compared to chimpanzees (Tomasello et al., 2012).

Humans in most societies rely on others for food, including through large-scale division of labor and cooperative foraging and hunting. Adolescence is a period in many societies where the group-level contributions individuals make within these systems begin to increase (Fuligni, 2019). Because adolescence in humans is a period where sensitivity to social feedback and value sharply increase (e.g. Rodman et al., 2020) adolescent human motivations to help and contribute to others (e.g. Fuligni, 2019) may be shaped by the prestige associated with these actions (Henrich and Muthukrishna, 2021).

In contrast to humans, chimpanzees rely far less on other adults for survival. For example, chimpanzees do not depend upon others to forage for their primary food—ripe fruit—on a daily basis. Yet, during adolescence, chimpanzees do show an increase in social behaviors that benefit others. Despite reduced interdependence and norm psychology, chimpanzees take actions that benefit others in the wild including grooming, sharing meat (Mitani et al., 2000; Mitani, 2009; Samuni et al., 2018), providing reassuring touch after a conflict, intervening in conflicts (Mitani et al., 2000; Aureli et al., 2000), waiting for others (Reddy and Mitani, 2019), joining one another on territorial boundary patrols which can lead to a lethal intergroup conflict (Mitani et al., 2000; Samuni et al., 2020a, 2021), and protecting others from lethal aggression during intergroup attacks (Sandel and Watts, 2021). Three main types of prosocial behaviors in chimpanzees increase and take on adult-like forms during adolescence: adoptive parenting of siblings after maternal loss (Hobaiter et al., 2014; Reddy and Mitani, 2019), the formation of reciprocal friendships and alliances (Nishida, 1983; Mitani, 2009), and participation in territorial boundary patrols (Langergraber et al., 2017).

Becoming Caregivers: Sibling Adoption.

Above. Typical sibling relationship. Early adolescent male Gus (middle) grooms his younger brother Denis (front) while receiving grooming from their mother, Sills (back). Photo by Jeremy Clift. Ngogo, KNP, Uganda, 2017



Above. Sibling parenting. Orphaned juvenile Holland presses his arm against the shoulder of his young adult brother, Buckner, who has been his adoptive parent since their mother, Lucia, died (Reddy & Mitani 2019). Photo by Kevin Lee. Ngogo, KNP, Uganda, 2017.

Chimpanzees have long maternal dependencies. They remain in frequent company with their mothers until age 12 which is many years after weaning (Pusey, 1983; Crockford et al., 2020; Reddy and Sandel, 2020; Samuni et al., 2020a, 2020b; Stanton et al., 2020). Sons remain in the same community as their mothers for life, accrue fitness benefits from their presence through the end of adolescence (16 years of age), and retain bonds with them into adulthood (Pusey, 1983; Takahata, 1990; Reddy and Sandel, 2020). Consequently, while growing up and even as adults, chimpanzees spend considerable time with their younger maternal siblings who are dependent on their mother and (like many primates with long maternal dependencies) typically form close bonds with them (Silk, 2002; Kapsalis, 2004). For maternal brothers who remain in the same community together for life, these bonds often last throughout adulthood (Langergraber et al., 2007). Older siblings often affiliate with their younger siblings by grooming them, playing with them, and occasionally carrying them during travel, but this reduces during adolescence when chimpanzees are gaining independence from their mothers; typically, during this time, adolescents and their younger siblings are beginning to spend less time together (Goodall, 1968; Pusey, 1983; Lonsdorf et al., 2018; Reddy and Mitani, 2019; Clark et al., 2021). Yet, in the event that mothers die, this changes completely.

If orphaned, adolescent chimpanzees often take on a parental role in the life of their younger sibling (Hobaiter et al., 2014; Reddy and Mitani, 2019). This adoptive parent role is taken on much more often by brothers than sisters because sisters emigrate to new communities during adolescence (and have in fact been reported to spend less time interacting with younger siblings in general during early adolescence, Lonsdorf et al., 2018) (Pusey, 1990; Hobaiter et al., 2014). When adolescent chimpanzees become primary caregivers, they have their younger siblings in almost constant company. The rate at which the two maintain spatial proximity, groom, engage in reassuring touch, and show vigilance for each other during travel increases dramatically. Adolescents also intervene to support their younger siblings in conflicts. Additional behaviors indicate that adolescents are emotionally motivated to provide this care. On occasion, older siblings show signs of separation distress, whimpering and screaming when parted from their younger siblings while still in a large subgroup of chimpanzees and not ceasing doing so until the two are reunited (Reddy and Mitani, 2019). Although adolescents are motivated to act as caregivers for their vulnerable younger siblings, this care may not be enough to buffer the against lifelong decrements in health, social status, and survival orphans face (Nakamura et al., 2014; Crockford et al., 2020; Samuni et al., 2020a, 2020b; Stanton et al., 2020). One study showed that orphaned juveniles were more likely to survive if adults adopted them but not necessarily if adolescents did (Hobaiter et al., 2014). Additionally, adolescent chimpanzees, particularly males who remain in the same community as their mothers for life, are still themselves dependent upon their mothers. Losing mothers before age 16 is associated with a reduced likelihood of survival (Stanton et al., 2020).

Forging Reciprocal Friendships.



Above. Reciprocal affection. Unrelated adolescent males Peewee (left) and Barron (right) mutually groom each other. Peewee and Barron share a strong social bond (Sandel et al. 2020). Photo by R.R. Ngogo, KNP, Uganda, 2014.



Above. Dependable alliances. Adult male Jackson, raises his fur and prepares to charge forward in an aggressive display. In the background, Jackson's close friend and ally Basie also has his fur raised and is prepared to charge forward together with Jackson. During adolescence and young adulthood, male chimpanzees gradually become part of coalitions and alliances with older males (e.g. Enigk et al. 2020). Photo by Kevin Lee. Ngogo, KNP, Uganda, 2017.

Until adolescence, chimpanzees' primary bonds are with their mothers. These bonds begin one-sided but become more reciprocal with age (Nishida, 1968; Pusey, 1983, 1990; Reddy and Sandel, 2020). As adolescents chimpanzees begin to form strong, reciprocal relationships with non-caregivers. As adults, these include many enduring, affectionate relationships with other adult chimpanzees who may or may not be their close genetic kin, and are often characterized by equitable grooming, meat-sharing, mating (when intersexual), and coalitionary support (especially when between males) (Mitani, 2009; Langergraber et al., 2007, 2013; Samuni et al., 2017, 2020, 2021; Bray and Gilby, 2020; Reddy and Mitani, 2020; Sandel et al., 2020; Reddy et al., 2021). Male chimpanzees in particular rely on their male "friends" as political allies, although certain chimpanzees may have little interest in rank-striving (e.g. Bygott, 1974). Adolescence may be a period where such interests are formed and interests may shape or be shaped by relationships (e.g., Bray and Gilby, 2020). For example, close male friends are often close in social status (and age) (Mitani, 2009).

Participation in Collective Action: Territorial Boundary Patrols.



Above. Territorial boundary patrol. Adult male chimpanzees hold each other as they hear and prepare to approach an "enemy" group while on a territorial boundary patrol. Photo by A.S. Ngogo, KNP, Uganda, 2018.

Adolescence is a developmental period where chimpanzees begin to participate at increased rates in territorial boundary patrols. Boundary patrolling is a collective activity where chimpanzees, predominantly males in some communities, quietly move along and across the boundaries of their community territory and into the territory of neighboring "enemy" groups (Watts and Mitani, 2001). If they meet neighboring groups they may kill or be killed by them.

Although many animals engage in forms of collective action (e.g. mongoose, meerkats, capuchins), the degree of coordinated intergroup killing in chimpanzees has few parallels other than humans and has been compared to human warfare. Boundary patrols are a highly dangerous, but important activity: By killing chimpanzees in other groups, chimpanzees expand their own territory and acquire new food resources (i.e. fruiting trees) (Mitani et al., 2010; Williams et al., 2004). In addition, boundary patrolling is an activity enacted by highly bonded individuals and it reinforces these bonds (Mitani et al., 2000; Samuni et al., 2017, 2020b, 2021, 2020, 2021). Urinary oxytocin levels rise on days of patrols (Samuni et al., 2017) and individuals engage in highly aroused touching, including frequent sociosexual behavior (Sandel and Reddy, 2021). Most male chimpanzees in groups participate in patrols (Langergraber et al., 2017; Massaro et al., 2022). This risky social participation, therefore, is part of becoming a successful adult. At the same time, there is interindividual variation in the frequency with which particular male chimpanzees participate in patrols (Langergraber et al., 2017) and adolescence may be a period where proclivities for patrolling are heightened in certain individuals over others.

social support they experienced from adults, which is replaced by increased aggressive and hostile behaviors rarely shown to juveniles (Box 2; Hayaki, 1988; Pusey, 1990).

Both females and males experience these heightened opportunities for learning and vulnerability—however, there is considerable sex-specific variation in how these manifest. Female chimpanzees disperse to and settle permanently in new communities during adolescence. Because relationships between chimpanzee communities are lethally hostile, when adolescent female chimpanzees emigrate, they must permanently sever ties with their mothers and all other group members (Box 2; Box 4; Nishida, 1979; Pusey, 1979, 1983, 1990). In contrast, male chimpanzees remain in their birth communities, with their mothers, maternal brothers, and other group members for life (Box 4).

3.1. Females

Female-biased dispersal, while characteristic of chimpanzees and

bonobos, is relatively rare in primates and social mammals broadly (Pusey, 1979; Kano, 1992; Isbell, 2004). Usually, male mammals leave the group in which they were born, while females stay (Packer, 1979; reviewed in: Isbell, 2004). The typical mammalian tendency for females to remain in the group and territories in which they were born and raised may relate to the demands of mammalian motherhood. Mammal mothers energetically invest more heavily in offspring than fathers, and mothers may thus benefit from taking advantage of their long-term knowledge of where and when to find food and to have the support of their own mothers and sisters (Trivers, 1972; Isbell, 2004).

It remains unclear what motivates adolescent female chimpanzees (and bonobos) to leave the group in which they were born, typically, after the onset of puberty (though potentially sooner after pubertal onset which itself occurs earlier in female bonobos than in chimpanzees, Behringer et al., 2014; Lee et al., 2020; Toda et al., 2022). Prior to their final dispersal, adolescent females show increased exploratory tendencies within their own communities (Box 2; Pusey, 1990). They travel further from their mothers to explore less familiar neighborhoods

Box 4 ADOLESCENT CHANGES IN PARENT-CHILD RELATIONSHIPS.

Mothers.



Above. Mothers in Early Life. Infant chimpanzee Cedar (right) receives grooming from his mother Kidman (left). Like all mammals, infants form close bonds with their mothers from birth. Photo by R.R. Ngogo, KNP, 2014.



Above. Mothers in Adolescence. Early adolescent female Ellen (front), rests in close proximity to her mother Bartoli (back). Ellen will eventually emigrate to a new community, severing ties with Bartoli forever. Photo by A.S.



Above. Mothers in Adolescence. Fitzgerald (left) grooms her adolescent son, Dylan (right). Although Dylan spends time apart from Fitzgerald he often whimpers upon separation from her (Reddy & Sandel 2020). Photo by A.S.



Above. Mothers in Later Life. Hutcherson (right), a prime adult male (28 years old), grooms his mother, Garbo (left) who is estimated to be 66 years old in this image. Video still by Kevin Lee.

Like most mammals, chimpanzees form their first social bonds with their mothers (Hinde, 1979). These bonds are very strong. Chimpanzee mothers are the primary and sole caretakers of their offspring, and infants remain in almost constant physical contact with mothers for the first year of life; they nurse and are carried during travel for five years on average, and even when they are weaned and walk independently as juveniles, they travel almost constantly together with mothers in the same subgroups that can change throughout the day (Goodall, 1968; Pusey, 1983; Goodall, 1986). Spending time together in the same subgroup is defined as being in “association.” Chimpanzees start to more frequently associate in subgroups apart from their mothers following the onset of puberty (Pusey, 1983, 1990; Reddy and Sandel, 2020).

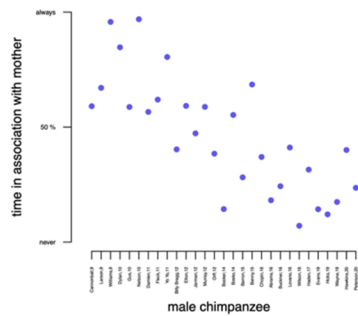
During this adolescent period, daughters typically emigrate permanently to new communities, severing ties with their mothers for the rest of their lives. In the event that daughters do remain in their natal groups and give birth there, however, they often retain primary bonds with their mothers and receive considerable fitness benefits from their presence (Goodall, 1986; Kahlenberg et al., 2008; Langergraber et al., 2009; Walker and Pusey, 2020). In general, however, female chimpanzee cease accruing fitness benefits from maternal presence around emigration age (Stanton et al., 2020).

In contrast, sons, who remain for life in the same groups as their mothers, accrue fitness benefits from maternal presence through adolescence up to age 16 (Crockford et al., 2020; Samuni et al., 2020b; Stanton et al., 2020). Although sons remain in the same communities as their mothers, they spend less and less time in association, or in the same subgroup with them, over the course of adolescence (Pusey, 1983, 1990; Reddy and Sandel, 2020). Therefore, they spend less time engaging in affiliative behaviors with them, including grooming, maintaining spatial proximity, and keeping track of each other during travel. At the start of adolescence, nearly all males have their mother as their top partner in the preceding behaviors, but by the start of young adulthood, only one-third of males do. Yet, even for the majority of adult males, affiliative relationships with mothers, though no longer primary attachments, endure (Pusey, 1983; Takahata, 1990; Reddy and Sandel, 2020). Nearly all adult sons associate in parties with their mothers occasionally, and if we examine affiliative behaviors during these periods, we see that older sons groom, maintain proximity to and keep track of their mothers during travel similarly to younger males. Importantly, adolescent and adult sons are typically the ones to initiate these interactions with mothers, illustrating their lifelong investment in these relationships (Reddy and Sandel, 2020).

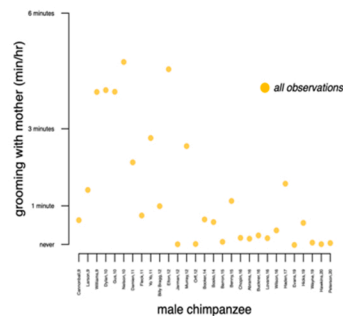
Although affiliative relationships with mothers endure, most sons seem to rely less and less on their mothers for emotional and coalitionary support as they approach adulthood (Sandel et al., 2020; Reddy and Mitani, 2020). For example, adolescent males receive regular support from their mother during aggressive conflicts (Pusey, 1983; Enigk et al., 2020; Reddy and Sandel, 2020) but adult males rarely do. Adolescent males often engage in reassuring touch (e.g. consolation: see Box 5) with their mothers following conflicts or other tense events, but adult males rarely do. Lastly, adolescent males often whimper or cry when separating from their mothers to follow other subgroups of chimpanzees (such as conflicted “crying” behavior is not observed in adolescent daughters; Pusey, 1983, 1990; Hayaki, 1988; Reddy and Sandel, 2020). These observations suggest adolescent male chimpanzees gradually become more emotionally secure spending time apart from their mothers, potentially because regular reassuring touch and coalitionary support in conflicts are components of the friendships they form outside of their maternal bonds, which increase in strength and number over the course of adolescence (Enigk et al., 2020; Sandel et al., 2020; Reddy and Mitani, 2020). Critically however, for adult sons of all ages, mothers are observed to continue to play an important role in moments of extreme hardship. Adult sons return to their mothers’ “core areas” or “neighborhoods” to search for food in times of scarcity (Murray et al., 2008) and anecdotally seek maternal company after extreme aggressive attacks and when healing from wounds (Pusey, 1983, pers. obs.). On occasion we have observed male chimpanzees to seek the company of their adoptive parents after such wounding events (Sandel, unpublished data).



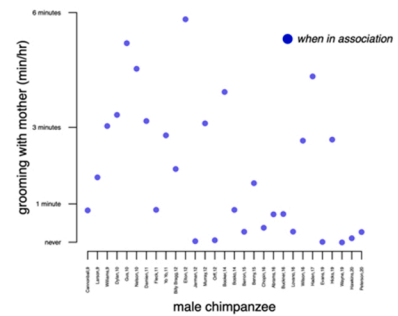
Above. Father (Figures) and Sons. Young adult male, Wes, grooms his biological father, Miles. Photo by A.S. Ngogo, KNP, Uganda 2014.



Above. Time in association between adolescent and young adult males and their mothers ($n = 29$ males). Reddy & Sandel 2020.



Above. Time spent grooming between adolescent and young adult males and their mothers during all observations of male subjects. Reddy & Sandel 2020.



Above. Time spent grooming between adolescent and young adult males and their mothers when male subjects were "home" or in association with their mothers. Reddy & Sandel 2020.

Fathers.

For chimpanzees, mothers are the primary caretakers. As we have discussed, adolescent and adult males may take on a caretaking role of orphaned youngsters who are often their maternal siblings (Box 3, Reddy and Mitani, 2019). But there is minimal evidence of biological fathers playing a caretaking role (Boesch et al., 2010; Hobaiter et al., 2014). Given the mating system of chimpanzees, where females mate with multiple males, it is expected that male chimpanzees cannot identify their offspring and offspring cannot identify their biological fathers.

Several studies have, however, shown that male chimpanzee show biased behavior toward their offspring. One study showed males play more often with their own infants than others at times when they are in association with all possible infant playmates (Boesch et al., 2006). Another study showed that for 6 months postpartum, female chimpanzees seek the company of their newborn infants' fathers (Murray et al., 2016). This likely represents an infanticide protection strategy on the part of mothers who may be seeking company of a male they think will protect them and their infant against such attacks as is seen in other primates (e.g. baboons: Smuts, 1985; Nguyen et al., 2009; Palombit, 2009). Male chimpanzees have indeed been observed to protect infants from infanticide, though these infants are not necessarily their own (e.g. Cibot et al., 2019; Lowe et al., 2019).

Fathers and "father figures" may play an important role for males during adolescence. Adolescent males must traverse uncertain social terrain as adult males replace affection with indifference and aggression (e.g. Pusey, 1990). As these adolescents attempt to socially integrate in a new way with adult males, adolescents often follow and groom specific relatively old males who relatively tolerate them compared to prime adults (Kawanaka, 1993; Nishida, 2011; Sandel, et al., 2020). These old males are sometimes called "mentors" as they facilitate adolescent males spending time in groups of adult males. A study from our research site, where a number of males live into old age (Wood et al., 2017) demonstrated that these mentor figures were the younger males' biological fathers (Sandel et al., 2020). These father-son relationships may be forged when sons are young, as their fathers and mothers may have close long-lasting bonds that contribute to mating and reproduction (but are not sexually exclusive) (e.g. Langergraber et al., 2013; Reddy and Mitani, 2020; Reddy et al., 2021).



Above. Father (Figures) and Sons. Young adult male, Wes, grooms his biological father, Miles. Photo by A.S. Ngogo, KNP, Uganda 2014.

(Fig. 3a), and sometimes visit and return from other communities (Pusey, 1990; Pusey et al., 2008; pers. obs.). During these exploratory excursions adolescent females (in contrast to males, see below; Box 4) notably show no signs of distress upon separation from their mothers (Pusey, 1990; pers. obs.). Adolescent females also regularly participate with (predominantly male) territorial boundary patrols, which can result in encounters with chimpanzees from other communities. During these inter-community encounters many participating chimpanzees run back and forth screaming and displaying aggressively (e.g. Watts and Mitani, 2001). Adolescent females in contrast, can remain relatively calm and curious. For example, they may sit still at the front lines with their arms crossed, looking toward the other community as others run chaotically around them (pers. obs.).

There is no evidence that female departure is caused by aggression from group members (i.e. “aggressive eviction”, see (Pusey and Packer, 1986)). In contrast, adolescent females receive hostility and on occasion severe aggression from females in the groups they attempt to join (Goodall, 1986; Nishida, 1989; Pusey, 1990; Pusey et al., 2008; Kahlenberg et al., 2008). For example, in one extreme case study, a young adolescent female chimpanzee, Schweini, born in the Kasakela chimpanzee community in Gombe National Park, Tanzania, joined a subgroup in the neighboring Mitumba community. In Mitumba, Schweini was severely attacked by resident females who hit and bit her repeatedly over the course of a day. Her wounds included a bite that exposed her skull. She returned the following day to her natal group where her mother and sister lived. However, nearly a year and a half later, Schweini attempted to join the Mitumba community again (Pusey et al., 2008). She was attacked again and returned to her natal group after only three days, eventually giving birth there two years later. Although Schweini’s case was unusually extreme (indeed a female Mgani, who emigrated to Mitumba during the same time period as Schweini received some aggression, but fought back, remained and integrated into the community—potential sources of such variation are discussed in Section 4) it highlights the motivation of female chimpanzees to join new groups

despite hardships involved (Pusey et al., 2008). This persistence suggests adolescent females may be motivated by some type of strong positive draw to explore or engage with an unfamiliar (indeed formerly “enemy”) group (i.e. “conspecific attraction” rather than “abduction,” or “aggressive eviction” from natal group as a cause for dispersal: (Pusey and Packer, 1986)). (Fig. 7).

While facing direct hostility from resident females, immigrant females must learn a wide range of crucial information about their new territory—including where to find food (i.e. fruiting trees, the primary food sources for chimpanzees; Wrangham, 1975) and safety (i.e. territory boundaries). They may learn partly through trial and error and partly by relying on new group members to share knowledge. Notably adolescent females spend considerable amounts of time socializing with males during this life stage who often support and protect them against aggression from resident females (Nishida, 1989; Kahlenberg et al., 2008; Pusey et al., 2008), and with whom they attempt to mate, though this is typically with adolescent male peers who (in contrast to adult males) have interest in mating with them (Muller et al., 2006, 2020; Watts, 2015; Reddy et al., 2021). Because adult males are “disinterested” in them, adolescent females are relatively freer from male harassment and sexual coercion than are adult females (Muller et al., 2006, 2007). Still, adolescent females may receive more aggression from males than they did as juveniles and they begin to regularly give pant grunts calls, indicating submission, to their male peers during this life stage (Reddy and Mitani, 2020).

Another source of social support for adolescent immigrant females appears to be from old resident females (Nishida, 1989; Sandel and Reddy, 2021). In certain populations, these older resident females are rarely aggressive to immigrant adolescent females; instead, most of the aggression immigrants receive comes from other young, relatively recent immigrant females who are themselves not well-established socially (Pusey et al., 2008; Nishida, 1989; Hansen, 2017, but see Kahlenberg et al., 2008). Accordingly, adolescent immigrants often follow and groom old resident females. These old females do not often groom

Box 5 SOCIAL TOUCH IN CHIMPANZEES.



Examples of social touch in wild chimpanzees including A) unidirectional grooming by an adult male to an adult female; B) mutual grooming between two adolescent males; C) mounting between two adult males upon hearing calls of another chimpanzee group; D) Embraces between an infant male and adult male who are reuniting

Photos: N. Chesterman, K. Lee, R. Reddy, Ngogo, Kibale National Park, Uganda 2014–2017

Touch represents a foundational component of social communication and social bond formation in humans, non-human primates, and many other mammals—particularly during formative periods of social development (e.g. [Cross and Harlow, 1965](#)). The vast majority of basic and translational research in these areas has focused on the formation of early infant-caregiver bonds. Across the lifespan of nonhuman primates, including chimpanzees, touch remains a key modality of affiliative dyadic social interaction between individuals of all ages. Two types of touch, **grooming** and **reassurance** appear to play a role in mediating arousal.

When **grooming**, individuals use their fingers and sometimes lips to stroke and search between the hairs of other individuals. Such gentle stroking movements activate the C-tactile system in humans and lower heart rate in macaques ([Aureli, Preston, and deWaal, 1999](#); [Jablonski, 2021](#)). It is unknown whether grooming has such effects in chimpanzees, whether these effects occur for both the giver and recipient of grooming, whether they occur at particular “optimal stroking velocities,” or with particular partners ([Jablonski, 2021](#)). Grooming occurs on a near daily basis in contexts where all chimpanzees are relaxed and resting. Chimpanzees also groom in moments of tension. For example, chimpanzees often groom prior to embarking on a territorial boundary patrol or while listening for neighboring “enemy” groups of chimpanzees during one (e.g. [Samuni et al., 2017](#)). Group members may also groom each other in the aftermath of an aggressive conflict among them (e.g. consolation and reconciliation: [deWaal & vanRoosmalen 1979](#)). In chimpanzees, and primates broadly, the frequency and equability of grooming between two individuals over time is often used to quantify the existence and strength of an affiliative bond between them ([Silk et al., 2003](#); [Smuts, 1985](#); [Mitani, 2009](#)). In several primate species, having strong social bonds as quantified by grooming is associated with improved longevity, health, and social status (e.g. [Silk et al., 2003](#); [Seyfarth and Cheney, 2012](#)). As newborns, chimpanzees primarily receive grooming from their mothers and maternal siblings. They can begin to groom other individuals around 2 years of age but this varies widely between individuals ([Nishida, 1988](#); [Bründl et al., 2021](#)). Grooming partners expand beyond family members in later infancy and especially in juvenility. Until the middle of adolescence, however, mothers are chimpanzees’ primary grooming partners ([Pusey, 1983, 1990](#); [Reddy and Sandel, 2020](#)).

Reassurance refers to a suite of touching behaviors categorized in early studies of wild chimpanzees including embracing, kissing, holding hands, mounting, and rubbing genitals ([Goodall, 1968](#)). What unifies these varied contacts is that they are interpreted to provide comfort in moments of distress or tension (i.e. “reassurance” or “consolation” ([de Waal and van Roosmalen, 1979](#))). Reassurance often involves contact between non-hairy skin on chimpanzees’ hands, feet, mouths and genitals and, compared to grooming, reassurance is swift and brief ([Aureli and Schino, 2022](#)). Reassurance is provided often by mothers to offspring (and adoptive caregivers to adoptees), and between unrelated individuals of all ages ([Goodall 1968](#); [Reddy and Mitani, 2019, 2020](#); [Reddy and Sandel, 2020](#)). It occurs often between individuals who share strong affiliative bonds ([Reddy and Mitani, 2020](#)). In particularly tense situations such as reunions, it also occurs between individuals who do not have strong social bonds; [Sandel and Reddy, 2021](#)).

adolescents in return. However, when adolescents are frightened the older females may provide reassuring touch that often includes socio-sexual behaviors ([Box 1](#); [Box 2](#); [Sandel and Reddy, 2021](#)).

The process of becoming successfully socially integrated as an adolescent female chimpanzee represents a high-stakes endeavor. When immigrant females give birth to their first infants (at 16 years of age on average: [Walker et al., 2018](#)) they are especially targeted for infanticide by both male and female group members. Chimpanzee infants are typically at risk for infanticide from group members for only a few weeks following birth. ([Box 1](#); [Goodall, 1977](#); [Pusey et al., 1997](#); [Arcadi and Wrangham, 1999](#); [Townsend et al., 2007](#); [Pusey and Schroepfer-Walker, 2013](#); [Walker et al., 2021](#); [Lowe et al., 2019, 2020](#); [Wood et al., 2017](#)). If immigrant females have secured dependable relationships by the time they first give birth, they may be better able to employ known social counterstrategies, such as seeking or receiving protection from group

members against infanticidal attacks during this postpartum period (e.g. [Murray et al., 2016](#); [Wellens, 2018](#); [Lowe et al., 2019, 2020](#); [Reddy, 2020](#)).

In addition to infanticide risks, females’ *lifetime status* can be established during adolescence ([Box 1](#); [Foerster et al., 2016](#)). A female chimpanzee’s status affects the resources and social opportunities that will be provided to her own offspring. High-status females have increased access to high-quality food, their offspring are more likely to survive, and they may be more likely to be socially connected rather than peripheral ([Pusey et al., 1997](#); [Wittig and Boesch, 2003](#); [Thompson et al., 2007](#)). Offspring of socially connected rather than peripheral females have many opportunities to socialize with non-family adults and peers prior to adolescence. Essentially, a female chimpanzee’s social actions in adolescence can potentially impact where she and her offspring can feed and socialize when she is forty years old (e.g. [Foerster](#)

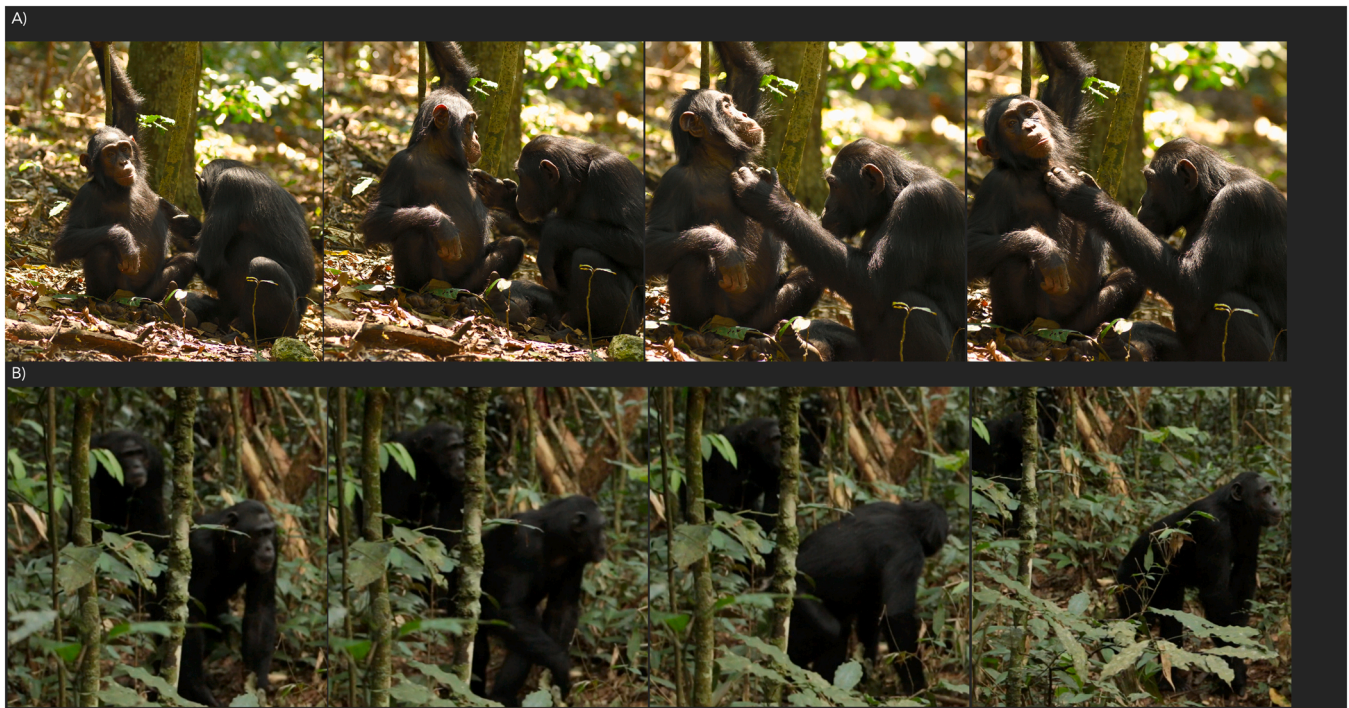


Fig. 6. An example of prosocial behaviors in chimpanzee adolescence. A young adolescent chimpanzee, Damien, demonstrates behavior that benefits others: A) At age 11, Damien (right) grooms his younger sister Etta (left) to whom he has acted as an adoptive caregiver since their mother's death. B) At age 12, Damien (right) joins his older brother Rollins (left) on a “war-like” territorial boundary patrol, a dangerous activity which can provide food resources to Damien's community. In stills from this video sequence, Damien looks back toward Rollins before moving forward.

Photos by Kevin Lee, Ngogo, Kibale National Park, Uganda, 2017. Video by A.S. Ngogo, Kibale National Park, Uganda, 2018.

et al., 2016). As adolescent female chimpanzees are attempting to integrate they are often navigating situations that are akin to making first-impressions—where the stakes appear to be extremely high.

3.2. Males

Male chimpanzees remain for life in their birth community with their mothers, brothers, and other group members (Pusey, 1979; Goodall, 1986). Still, adolescent males have much to learn and face many risks and vulnerabilities as they interact in new ways with relatively familiar individuals.

Adolescent males begin to travel apart from mothers and follow adult males. In contrast to adolescent females, as adolescent males separate from their mothers they show conflict and distress—often whimpering and looking back toward their mothers as they walk away and follow adult males (Hayaki, 1988; Pusey, 1990; Reddy and Sandel, 2020). Adult males, who have extremely affectionate bonds with each other (e.g. Mitani, 2009; Box 3) and who previously showed affection to these young males when they were infants and juveniles, withdraw affection from adolescent males and begin to target them with aggression instead (Box 2; Hayaki, 1988; Goodall, 1986; Pusey, 1990; Nishida, 2011). In addition, adolescent male chimpanzees expose themselves to even more dangerous forms of aggression when they join these adult males into dangerous situations such as territorial boundary patrols which they may not have participated in at earlier ages (e.g. Box 2,4; Langergraber et al., 2017). Still, adolescent males persist in following these adult males as they attempt to seek entry into the close-knit adult male social world. In contrast to prime-aged adult males in this “social world,” adolescents tend to avoid asserting dominance over older males or even their male age peers (Box 2; Hayaki, 1988; Sandel et al., 2017). They may delay vying for high status in the male dominance hierarchy until their early twenties (Box 2; Goodall, 1986; Kawanaka, 1993; Watts, 2018). This delay in status engagement emphasizes the complexities of “earned” status for chimpanzee males. By remaining on the outskirts of

social gatherings and avoiding aggression, they have an extended period in which to observe and learn (Box 2 Fig. 3b,c).

Other types of social relationship formation may be important for adolescent male chimpanzees in ways that can help to scaffold this learning and mitigate against some vulnerabilities from interacting with prime-aged adult males who socially reject them. While avoiding prime adult males, adolescent males often affiliate with females and with their male peers, who can groom them reciprocally (Reddy and Mitani, 2020; Sandel et al., 2020; Reddy et al., 2021). Importantly, adolescent males also often groom old adult males who have reduced involvement in aggressive competition themselves and are sometimes referred to as “mentors” (Kawanaka, 1993; Nishida, 2011; Sandel et al., 2020). Like the old female chimpanzees who are followed by adolescent immigrant females, old male mentors seldom groom adolescent males in return but tolerate them, permit them to follow, and can provide reassuring touch in frightening situations (Box 2,5; Sandel et al., 2020). It is not entirely clear what draws adolescent chimpanzees to particular mentors but the fact that they are often old males who have survived longer than many of their peers, suggests it may be some form of skill-related prestige as well as reduced threat (Henrich and Gil-White, 2001; Nishida, 2011). Another component of adolescent males' mentor selection appears to be past familiarity. For example, mentors may be males who adolescents grew up knowing well because these males shared close bonds with adolescents' mothers (e.g. Langergraber et al., 2013; Reddy and Mitani, 2020; Reddy et al., 2021). Indeed, mentors are often “familiar” males from infancy and juvenility, and likely to be adolescent males' biological fathers, if they are alive (Box 4; Sandel, 2017; Sandel et al., 2020; Bray et al., 2021b).

Although adolescent male chimpanzees avoid male-male status competition, they work to dominate all females in their group (with the exception of their mothers) by the time they reach adulthood (Goodall, 1986; Pusey, 1990; Nishida, 2003, 2011; Reddy and Mitani, 2020; Enigk et al., 2021; Reddy et al., 2021). Adolescent males make repeated “harassment” attacks of peer and adult females which females initially

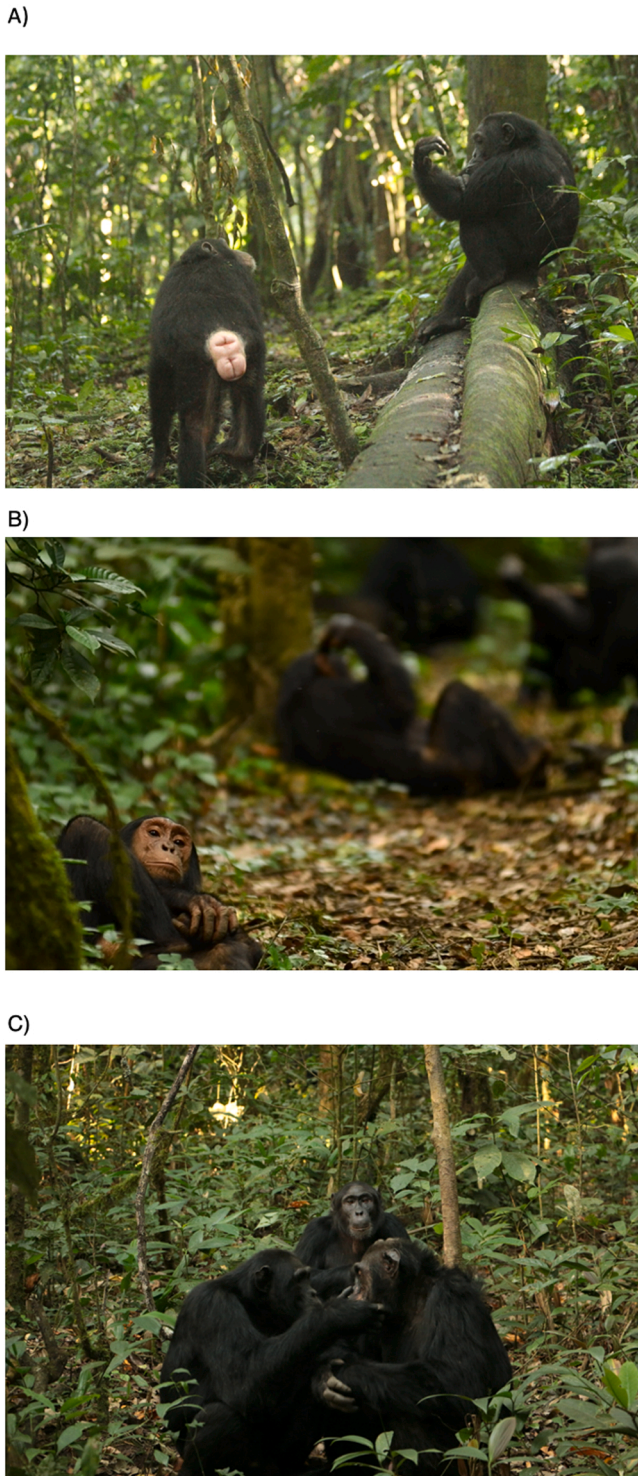


Fig. 7. Examples of social exploration and social rejection during chimpanzee adolescence. a) Rosa, an adolescent female chimpanzee (left) approaches a young adult male, Haden (right), while exploring outside her neighborhood. Haden grooms his arm and does not respond to Rosa's approach. b) Gus, an adolescent male chimpanzee sits at the outskirts of a social gathering. c) Damien, an adolescent male chimpanzee observes in close proximity as two adult males groom each other, without receiving grooming himself. Photos by R.R., Kevin Lee, and A.S. Ngogo, Kibale National Park, Uganda 2015 – 2018.

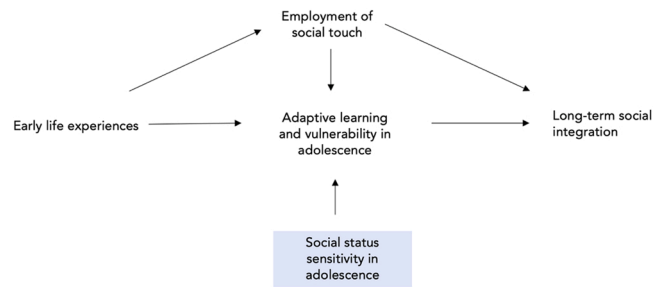


Fig. 8. A conceptual framework for investigating (1) how social status sensitivity can guide social learning during chimpanzee adolescence while simultaneously exposing adolescents to vulnerabilities (i.e. rejection), (2) how social touch (Box 2) can buffer against such vulnerabilities and promote persistence and learning in uncertain situations, and (3) how both learning, vulnerability and proclivities for social touch during adolescence can be shaped by early life experiences and contribute to later life social outcomes.

ignore, then retaliate against before finally regularly giving submissive pant-grunt vocalizations in greeting to particular males (e.g. Nishida, 2003). Once males become dominant, the aggression they direct toward females begins to function as sexual coercion, earning them mating opportunities (Smuts and Smuts, 1993; Muller et al., 2007; Feldblum et al., 2014; Kaburu and Newton-Fisher, 2015; Reddy et al., 2021; Watts, 2022). However, this type of sexual intimidation is not always successful (Stumpf and Boesch, 2010; Kaburu et al., 2015). Male aggression is most sexually coercive when directed toward females with whom males have developed strong affiliative bonds (Reddy and Mitani, 2020; Reddy et al., 2021). Males begin to forge these affiliative and relatively reciprocal, yet aggressive (on the part of males) bonds with females during adolescence. They increase in strength and number with male age (Reddy and Mitani, 2020). In early adolescence, when males do not yet dominate females or have a place in the male dominance rank hierarchy, these affiliative bonds, especially with adolescent female peers, are critical routes to reproducing (Reddy et al., 2021). Males who form such relationships in early adolescence can father offspring years earlier than their peers (Reddy and Mitani, 2020; Reddy et al., 2021).

4. Sources of individual variation in adolescent behavior and adult social outcomes

There is considerable interindividual variation in the ability of adolescent chimpanzees to form strong and reciprocal social bonds outside of their maternal families. As described in the previous section, the formation of successful social relationships in adolescence has consequences for immediate and long-term social and reproductive success (e.g. Reddy et al., 2021). Variation in chimpanzee social integration need not be viewed as pathological but rather as variation in strategies based on preferences and skills, in ways that may in part be shaped by early life experience (e.g. varied reproductive strategies: Gross, 1996; Langergraber et al., 2013; Reddy et al., 2021; Silk et al., 2020). Here, chimpanzees face considerable variation in the social (and nutritional) resources they are afforded as infants and juveniles as well as the threats and adversities to which they are exposed. Because motivations for social exploration appear to increase after puberty onset in chimpanzees, adolescence may provide a potential window of opportunity for resilience against these adversities incurred in early life. Below, we detail several sources of chimpanzee early life adversity which could be mitigated against during adolescence.

4.1. Conflict and instability

Conflict and instability both between and within chimpanzee communities can shape early life development. Heightened between-community pressure is associated with reduced infant survival

(Lemoine et al., 2020b). Additionally, chimpanzees born during times of within-group political instability or under a particularly aggressive alpha male's reign, are exposed to heightened aggression at a broad level compared to chimpanzees born in times where the hierarchy is stable (Foster et al., 2009).

4.2. Status and resource access

Status and food resources available to chimpanzees vary on a group and individual basis. Larger chimpanzee groups have increased territory which they acquire by patrolling their own borders and terrorizing or making lethal attacks on chimpanzees of other communities (Watts and Mitani, 2001; Williams et al., 2002, 2004; Mitani et al., 2010; Wilson et al., 2014; Samuni et al., 2020a, 2021; Lemoine et al., 2020a). Larger territories often have increased food resources, and in chimpanzee communities with more abundant resources individuals show improved energy balance, survival rates, and longevity (Williams et al., 2002; Thompson et al., 2009; Potts et al., 2011; Wood et al., 2017).

Within a community's territory, individual food access is determined by dominance status (Pusey et al., 1997; Wittig and Boesch, 2003; Thompson et al., 2007). In several chimpanzee populations, females have particular regions, called "neighborhoods," or "core areas," within the community territory where they reside and primarily feed with their dependent offspring (e.g. Williams et al., 2002; Mitani and Amsler, 2003). Core areas vary in food quality and females compete for them, with high-status females living in the highest-quality core areas (Pusey et al., 1997; Thompson et al., 2007; Kahlenberg et al., 2008; Pusey and Walker, 2013; Miller et al., 2014). Maternal dominance status is additionally associated with improved offspring survival, reproductive success, and dominance status among peers prior to adolescence (Pusey et al., 1997; Pusey and Schroepfer-Walker, 2013; Markham et al., 2015).

4.3. Maternal social connectedness

Mothers' social proclivities profoundly impact the experiences their offspring have as infants and juveniles, and these proclivities vary widely between female chimpanzees, including in relation to dominance status, described above (Murray et al., 2014; Wellens, 2018). Some infant and juvenile chimpanzees may rarely interact with peers or adults outside of their maternal siblings prior to adolescence, while others may grow up playing constantly with non-family peers and regularly receiving affection (e.g. tickling, embraces) and shared meat from high-status adults, who, for males, may become their mentors in adolescence (Sandel, 2017; Sandel et al., 2020). Consequently, chimpanzees whose mothers avoid outside-family socialization appear to develop with a much more constrained range of social experiences as infants and juveniles compared to peers whose mothers are highly socially connected.

4.4. Maternal loss

An extreme form of adversity in chimpanzees' early life is maternal loss. Chimpanzees rarely survive to adulthood if they lose their mothers before weaning age. Maternal loss even after weaning and throughout adolescence (up to 16 years) is associated with decrements in growth, survival, reproduction, and social status (Nakamura et al., 2014; Crockford et al., 2020; Samuni et al., 2020a, 2020b; Stanton et al., 2020). Orphans demonstrate acute depression-like symptoms and heightened distress when mothers die; in one report, an 8-year-old chimpanzee refused to eat or leave his mother's body, despite his elder siblings' attempts to make him follow them, and soon after died (Goodall, 1983). Recently orphaned juveniles also whimper and seek increased physical comfort from others (Reddy and Mitani, 2019). In many cases, juvenile chimpanzees who survive maternal loss are adopted by an adult who is likely to be an older maternal sibling if they have

one, or an unrelated adult male (Boesch et al., 2010; Hobaiter et al., 2014; Reddy and Mitani, 2019; Box 3).

5. Future directions: understanding adolescence as a sensitive window for adaptive social learning, prosocial behavior and resilience

Given that adolescent chimpanzees appear to demonstrate new motivations for exploring social interactions, adaptive learning, and forming new relationships, they may provide new insights into understanding adolescence as a period of opportunity for social exploration and learning in ways that can contribute to resilience following early life adversity. New relationships can be forged which may mitigate earlier hardships. There is already evidence for such resilience in long-term chimpanzee studies. For example, although orphans face many challenges, as detailed above (e.g. Hobaiter et al., 2014; Nakamura et al., 2014; Crockford et al., 2020; Samuni et al., 2020b; Stanton et al., 2020), they can also overcome them. For example, orphans who survive to adulthood seem to eventually recover from certain immediate impacts such as heightened activation of the HPA axis (as measured by diurnal urinary cortisol slopes, Girard-Buttoz et al., 2021). In our study population some orphans go on to become reproductively successful and socially integrated (Sandel et al., 2020; Reddy and Mitani, 2020; Reddy et al., 2021).

Understanding developmental pathways to resilience among wild chimpanzees—and how adolescent-specific proclivities may promote both learning opportunities as well as vulnerability on a broad level—may provide unique insights relevant to the underpinnings of the development of adolescent proclivities in humans. For example, human adolescents show increased sensitivity to social status and social rejection, yet, in contrast to adults, report continuing to "like" individuals who have rejected them (Rodman et al., 2017). In chimpanzees, a sensitivity to others' popularity and motivation to engage popular individuals, even if initially rejected, may be critical to providing experiential opportunities to learn how to earn social inclusion. For emigrating female chimpanzees in particular who are in an entirely new social environment where they must make a lasting "first impression," salient cues from individuals that convey social rank and social connectedness may be critical to quickly identify mentor females whom adolescents can follow to learn about their new and complicated socioecological landscape.

Hypotheses about developmental changes in social proclivities could be explored by conducting experimental research with zoo and sanctuary-living chimpanzees. For example, recent experimental work with sanctuary-living chimpanzees has uncovered that proclivities for risky decision-making begin to increase in adolescence and peak in young adulthood. Chimpanzees in this experiment chose between a "safe" option (one food reward) and "risky" option (zero or two food rewards at 50/50 chance) presented to them by a human experimenter (Haux et al., in press).

Additionally, for adolescents of both sexes, support in the form of reassuring touch and grooming (Box 5) with mentors and others might mitigate excessive arousal in risky and uncertain social situations and enable adolescents to successfully navigate these situations to join rather than avoid gatherings and to thus, gain additional valuable social learning experiences (e.g. Sandel et al., 2020; Sandel and Reddy, 2021). Adolescents' own proclivities and developmental of skills for social touch might additionally reduce the likelihood of social rejection, especially in the form of aggression. In the long-term, engaging in social touch with mentors and others, and being able to effectively mediate arousal may facilitate adolescents forming long-term reciprocal dyadic social bonds that are central to adult social success (Fig. 8). Future research can investigate these processes in wild chimpanzees.

These advances in characterizing the behavioral and social motivational changes during adolescent development in wild chimpanzees are well aligned to the broad goals of this special issue: to explore novel and

translational findings on puberty and brain maturation in humans and nonhuman species. Field studies of wild chimpanzees represent a promising approach to gaining novel insights on the evolutionary and neurobehavioral underpinnings of puberty and a cross-species perspective on this extended multi-year phase of adolescent learning and development. In chimpanzees, this extended period of social exploration creates not only risks, but also opportunities, particularly in relation to social, affective and motivational learning. These patterns are in line with growing evidence from studies of human adolescent development highlighting changes in social and affective processing at puberty; these findings include evidence that a) sex-specific developmental changes in reward sensitivity and sensation seeking in adolescence are associated with gonadal hormones and pubertal development (Harden et al., 2018); b) affective neuroscience research indicating that maturational changes in striatal activation and cortico-striatal functional connectivity to cues predicting rewards are positively associated with pubertal status and levels of pubertal hormones (Ladouceur et al., 2019); and c) that early adolescence/puberty appears to be a developmental window of heightened salience of social and emotional information processing in ways may confer important advantages for adaptive learning of social behavior (Rosen et al., 2018).

Finally, this work may also provide new insights into understanding adolescence as a sensitive period of learning relevant to translational research on resilience in human development. For example, recent research suggests that adolescence represents a period of heightened sensitivity to the *caregiving environment*—in ways that have important implications for recovery following early-life adversity (Colich et al., 2021). This evidence is consistent with evidence supporting the idea that adolescence is a period of heightened plasticity in stress response following early-life adversity (Gunnar et al., 2019). Taken together, these emerging insights into social learning in wild chimpanzees represent a promising approach to contributing in new ways to this exciting frontier—advancing a more integrated understanding of puberty and brain maturation in humans and nonhuman species.

Funding

R. B. Reddy was supported by a fellowship from the Mind Brain Behavior Interfaculty Initiative at Harvard University.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data Availability

No data was used for the research described in the article.

Acknowledgements

We are grateful to the Uganda Wildlife Authority, Makerere University Biological Field Station, and all members of the Ngogo Chimpanzee Project for their facilitation, mentorship and collaboration which made all insights we learned from the Ngogo chimpanzees in Kibale National Park, Uganda possible. We especially thank Samuel Angedakin, John Mitani, Kevin Langergraber, David Watts, Alfred Tumusiime, Ambrose Twineomujuni, Godfrey Mbabazi, Lawrence Ndagizi, Brian Kamugyisha, Chris Aliganyira, Dr. Jacob Negrey, Carolyn Rowney, Jeremy Clift, Charles Birungi, James Tibisimwa, Charles Businge, Diana Kanweri, Kahlunga Davis, and the late Jerry Lwanga. We thank Kevin Lee, Nathan Chesterman, Isabelle Clark and Jeremy Clift for sharing their beautiful photos for this article. We thank Katie McLaughlin, Alexandra Rodman, Daniel Pine, Linda Wilbrecht, and all members of the Stress & Development Laboratory, Pan Lab and Culture, Cognition,

Coevolution Lab at Harvard University for discussions, feedback, and insights that helped us to develop the ideas we present here. We thank Daniel Pine, Gabrielle Bunnell, and two anonymous reviewers for feedback that has improved this manuscript. We also thank Linda Wilbrecht for the opportunity to submit to this special issue. Last, we are grateful to Anne Pusey for discussions about chimpanzee adolescence and behavior beginning more than a decade ago that have inspired and influenced our research ever since.

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