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The Search for Love in Human Evolution: Primate Social Bonds and a New Science of Emotion

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ABSTRACT

Love defines the human experience but often defies scientific study. Biological anthropologists flirt with the topic of love by studying monogamy and affiliative relationships. The interest in monogamy, I argue, is misplaced. But the interest in affiliative relationships is productive and deserves greater theoretical and methodological innovation. Social bonds have been carefully described for decades by primatologists, but I suggest that we still lack conceptual clarity and the crucial data needed to distinguish them from other types of relationships. A deeper understanding of social bonds, and pair bonds in particular, will be possible through the application of new methods to study affective states, or "emotions," in wild primates and other animals. By studying the emotions that underly various relationships, we will make progress toward answering prevailing questions about the origins and future of love, romance, and friendship.

1 | Introduction

Biological anthropologists have a long-standing interest in monogamy (e.g., Benshoof and Thornhill 1979; Quinlan 2008; Chapais 2008). When in human evolution did male and female reproductive partners begin forming enduring, cooperative relationships? The interest is warranted because this social and reproductive pattern is rare among mammals and may have had a big impact on many other human traits, including wide kinship networks, communal care of infants and children, cooperation across groups, and our distinct life history patterns (e.g., Low 2003; Chapais 2008, 2013; Kramer and Russell 2015; Schacht and Kramer 2019). Paleoanthropologists thus look to the fossil record for clues as to when in our evolutionary history hominin species might have been monogamous and why (e.g., Lovejoy 1981, 2009). Primatologists look to other species where a single male and female pair live and mate together, which is rare among mammals but somewhat more common among primates, to see if any similarities exist across species that could explain why natural selection may have favored monogamy (e.g., Fuentes 1998; Reichard and Boesch 2003; Lukas and Clutton-Brock 2013; Opie et al. 2013). An understanding of the reproductive and grouping patterns of humans and other primates is valuable for many reasons, but the interest in monogamy in human evolution may be misplaced and misconstrued (Fuentes 1998, 2002, 2022; Reichard and Boesch 2003; Ryan and Jetha 2012). This is largely due to ambiguities in what is meant by monogamy.

What exactly do we mean by monogamy, and why do we care about it? "Certainly, to talk about monogamy is to talk about virtually everything that might matter," writes the psychoanalyst Adam Phillips (1996) in his popular book of aphorisms on the subject. Monogamy is a term we use in our everyday lives, and it is tied up with love, marriage, sexuality, and more. It is difficult to separate monogamy from heterosexual marriage, which is a norm across many human populations, but does not require love or sexual exclusivity (Levine and Silk 1997; White et al. 1988;

Low 2003; Henrich et al. 2012; Starkweather and Hames 2012; Scelza 2013, 2022). Given the personal, cultural, and ethical complexity, it is important to clarify what we mean by monogamy, especially if we are to study it across human populations and across other species and opine about its evolution.

Many studies on monogamy have not been so clear on their definitions (e.g., Kleiman 1977; Wittenberger and Tilson 1980), but over the past three decades, primatologists have taken considerable effort to clarify these concepts (e.g., Fuentes 1998, 2022; Reichard and Boesch 2003; Tecot et al. 2016; Huck et al. 2020; Fernandez-Duque et al. 2020; Bales et al. 2021). *Monogamy* is understood as a mating system: a relatively exclusive pattern of reproduction between one male and one female. This is distinct from *pair living*, a social system in which one adult male and female travel together and occupy the same range. And both are distinct from *pair bonding*, a strong social and emotional relationship, often between an adult male and female who often reproduce together and share in offspring care. With these three distinct concepts in mind, which of these "monogamies" are we actually interested in (in our personal lives and as biological anthropologists)? I think it is the pair bond. In a sense, we are really interested in love (Finkel and Eastwick 2015; Fletcher et al. 2015).

2 | How Can We Study Love?

Although discussions of love are largely reserved for our personal lives and the stuff of art, poetry, and spirituality, there is a longstanding interest in the science of love. To what extent is our capacity for love based in our biology, shared with other species, and shaped by evolution (Fisher 2016, Fisher 2004; Machin 2022; Lents 2025)? To date, much of the scholarship on love, especially "romantic love," has been done by psychologists. Neuroscientists have also contributed to this work by studying the neurobiology of attraction and relationships in humans (e.g., Fisher et al. 2006; Rinne et al. 2024), and in the similar attachments formed by other animals, especially rodents (e.g., Carter 1998; Bartels and Zeki 2000; Insel and Young 2001; Walum and Young 2018). Although this expansive literature has offered numerous insights, several problems exist. Notably, psychologists often rely on local and contemporary notions of love without critical reflection on the cultural and political forces that may shape these concepts. In addition, neuroscientific studies on rodents are appealing (because it is possible to conduct invasive studies of their brains and neurochemistry), but it is not clear whether whatever is going on with mice and voles as they copulate, groom, and sit near each other in a lab cage is comparable to the psychology and emotions that animate human love.

For a proper scientific study of love, or the relationships that seem to reflect love, we need (1) greater conceptual clarity and (2) more detailed description of the phenomena we are studying. We need this for our own species, with definitions that resonate with our actual experience of love in all its manifestations, and methods that capture meaningful variation in relevant behaviors and emotions. We also need definitions and methods that are relevant and can be applied across species. In this regard, biological anthropologists may be in a valuable position to contribute. As experts in human evolution, we may be able to temper the impulse of some psychologists to make far-reaching and unfounded claims about the evolutionary processes shaping human behavior. We take a cross-cultural perspective, drawing on human behavioral ecology, cultural evolution, and with our disciplinary origins and departmental adjacency to cultural anthropology. And we study a range of primate species, both in the wild and in captivity, including detailed, long-term studies of their social behavior and physiology. Primatologists also offer a disciplinary bridge to psychology and neuroscience, where most of the scientific scholarship on love occurs.

3 | Conceptual Clarity on Love and Relationships

Psychologists have offered several frameworks for studying love (e.g., Sternberg and Barnes 1988; Fehr et al. 2009; Berscheid 2010; Finkel et al. 2017). For example, Sternberg (1986) identified three main components of love: (1) intimacy, which includes feelings of connectedness or closeness, (2) passion, which includes physical attraction and sexual activity, and (3) commitment, which includes the decision to love someone and be committed to them. The presence of one or multiple components constitutes different types of love, including romantic love, companionate love, fatuous love, and consummate love. Other psychologists have offered similar broad categories, including romantic, companionate, compassionate, and adult attachment love (Berscheid 2010). What constitutes sexual attraction compared to other forms of attraction or bodily pleasure? Van Anders (2015) breaks down sexuality into eroticism and nurturance, which are distinct from lust and love, and these manifest in a range of relationships and can occur outside relationships with others. Separating love into these categories and specifying it deserves additional scrutiny (e.g., Diamond 2004). Just as primatologists distinguish among monogamy, pair living, and pair bonding, any science of love should disentangle the emotional, sexual, and material components of different relationships (Figure 1).

Clarifying a conceptual understanding of loving relationships requires attention to culture, history, and the variety of ways people experience their social world. Different types of love may manifest variably in different relationships—with romantic partners, family, friends, and others—and love may be absent in many of these cases (e.g., in marriages, families, and with people we may nevertheless call our friends). These categories are not so rigid. For example, friendships may contain sexual or erotic desire (Kaplan and Keys 1997; Bleske-Rechek et al. 2012; Ghisyawan 2016). What we often label as friendship may include more intimate, loving, and important relationships (Box 1). For example, "queerplatonic" relationships refer to intimate, life partnerships that do not have a sexual component (Chasin 2015). Queer perspectives may help disentangle the sexual, emotional, and material components of relationships (Halperin 2019; Hammack et al. 2019; Kauth 2020; Winer 2024), and more integration in psychology and behavioral biology will be fruitful (e.g., Van Anders 2015).

Integrating ideas across disciplines has been key for studies of love, and studies of primates are especially valuable. Attachment theory identified just how important mothers and other caretakers are to the development of human infants (Bowlby 1958, Ainsworth 1979). Attachment theory was heavily

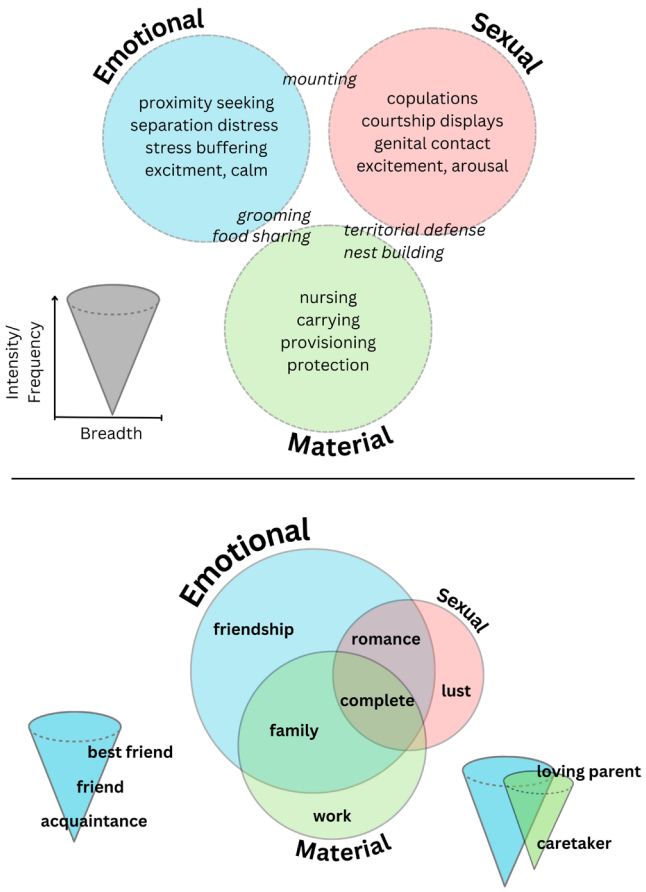

FIGURE 1 | A conceptual framework for understanding the main categories of love in humans (and, potentially, other animals).

BOX 1 | More than friends.

Bonds of friendship are not all that different from bonds of romance. Ethnographic evidence supports the similarities between some same-sex friendships and marriage, as in the "blood brothers" in some cultures (Beattie 1958) and "marriages" between women in other cultures (Njambi and O'Brien 2000). Notably, poetry, literature, and philosophy celebrate passionate friendship; in many respects, the ideal friendship as defined and described from the ancient world to present day bears a striking similarity to contemporary notions of romance. The first written story in human history is one of friendship between two men, Gilgamesh and Enkidu. Gilgamesh was destined to find a friend—"you will love him as a woman and he will never forsake you" (Sandars 1972). After Gilgamesh and Enkidu meet and grapple, they become friends: "They had embraced and made their vow/ To stay together always/No matter what the obstacle" (Mason 2003). Similar passion is recounted in the Bible, as David loved Jonathan, "he loved him as he loved his own soul" (1 Samuel 20:17). And when Jonathan died, David lamented: "I am distressed for thee, my brother Jonathan; very pleasant hast thou been unto me. Thy love to me was wonderful, passing the love of women" (2 Samuel 1: 26). Think about your friends, which can outlast romantic partnerships and even marriages. Could our loneliness epidemic be due, in part, to the fact that we lack the social, economic, and political support for friends that we have for marriage?

influenced by research on primates, including experimental studies by Harlow (1958) who called for a scientific study of love. Bowlby's work on attachment coalesced from his conversations with Hinde, who was a trailblazer in the systematic study of animal behavior (Stevenson-Hinde 2007; van der Horst et al. 2007). Hinde also offered a clear, conceptual understanding of social "relationships" that could be applied across species. Relationships, simply put, are repeated interactions across time between known individuals which can vary on several dimensions, including frequency, duration, reciprocity, and predictability (Hinde 1987; Silk et al. 2013). It is in these relationships that scientists have a chance to make progress studying love.

3.1 | Social Bonds in Primates

A major focus in field primatology has been on social relationships, including the strongest and most affiliative relationships, or "social bonds," which have been likened to "friendship" (Washburn and DeVore 1961; Smuts 1985; Silk 2002). Although there is no consensus on a definition, social bonds are often considered affiliative relationships that are especially frequent, enduring, reciprocal, and predictable. For example, Seyfarth and Cheney (2012) used "friendship" as shorthand for "close, enduring social bonds that are not directly related to mating: bonds among females, for example, or among males." Similarly, Brent et al. (2014) used social bond and friendship interchangeably, defining both as "pairs of individuals that engage in bidirectional affiliative (nonaggressive, non-reproductive) interactions with such frequency and consistency so as to differentiate them from non-friends." Dunbar (2018) defined bonded relationships as "long-lasting rather than casual, involve close attention to the partner [...], and a constant desire to be physically with the partner." The strongest example of a social bond includes those between mothers and infants and in cases of pair bonds.

Our conceptual understanding of social bonds benefits from definitions of pair bonds. Whereas social bonds have largely been analyzed from behavior alone, pair bonds often include an affective component (Smuts 1985; Fuentes 2002; Silk et al. 2013; Bales et al. 2021). Building on the work of other primatologists and behavioral ecologists, Bales et al. (2021) defined pair bonds in a way that could be applied across species. They define pair bonds as strong and enduring relationships between two adults (often a male–female duo, but not necessarily so). The relationship must include some behavior specific to that pair, and there must be an affective or "emotional" component, such as attraction, stress buffering, and separation anxiety. This definition fits with a growing consensus in primatology that pair bonds are best understood as a particularly strong, enduring, and emotionally charged social bond (Fuentes 2002; Dunbar 2014). A reevaluation of the literature on primate relationships raises the possibility that some social bonds merit the classification as pair bonds.

3.2 | An Overlooked Example of Pair Bonds in Chimpanzees

Some of the strongest evidence for social bonds in primates comes from chimpanzees, where enduring, cooperative relationships

are more than mere exchange relationships (Mitani 2009) and may warrant the term "friendship" (Silk et al. 2013). I also suggest that some of the strongest and most enduring bonds between some adult male chimpanzees are best understood as pair bonds (Sandel 2023). Adult male chimpanzees exhibit preferential proximity and grooming relationships which can last several years and, in some cases, over a decade (Mitani 2009; Bray and Gilby 2020). These relationships include a diversity of cooperative behaviors, including hunting, territorial patrols, coalitions, and sharing of food (Watts and Mitani 2001; Samuni et al. 2018, 2021; Bray et al. 2021). In addition to preferentially socializing and cooperating year after year, several lines of evidence support an affective component to these relationships. For example, one study found that grooming between long-time partners—between males and in other enduring duos—was associated with an increase in oxytocin (Crockford et al. 2013). Other studies have found that cortisol levels, a hormone associated with social stress, were lower when in the presence of bonded partners (Wittig et al. 2016). Several behaviors, including grimaces, embraces, genital contact, and thrusting during mounts, are suggestive of high arousal and empathy (Sandel and Reddy 2021). Are the strongest social bonds between chimpanzees actually pair bonds? If this is the case, it has important implications for how we infer the evolution of pair bonds in humans.

Pair bonds are thought to be unique to the human lineage because our closest ape relatives, chimpanzees and bonobos, do not form especially strong social bonds with their reproductive partners. But it is possible that pair bonds existed in our last common ancestor with chimpanzees and bonobos. Rather than being in the context of reproductive partners, however, pair bonds may have occurred in what we have been calling "friendship" (Sandel 2023). The cognitive, neural, and hormonal mechanisms that enable pair bonds in humans today may have evolved first for social bonds and pair bonds in our ape ancestors, especially those between same-sex pairs. Those mechanisms were later co-opted in human evolution for the sake of bonds between reproductive partners (Sandel 2023). If this is the case, what we often think of as heterosexual romance may find its origin in homosexual friendship. We often think of the attraction and attachment between men and women to be intuitive, reflecting a natural order. But this is not the case when we look across the animal kingdom. Many males and females come together to mate, but they do not form a special social relationship. The strongest bonds in the animal kingdom are often between mothers and offspring, maternal half-siblings, and in some group-living species between unrelated individuals. We may be overlooking important social bonds, including pair bonds, that manifest in different contexts, including between same-sex pairs. To test whether some pairs of adult male chimpanzees actually exhibit pair bonds, we need additional data on the affective states underlying relationships. Herein lies one of the major challenges. It is very difficult to study emotions in animals.

Primatologists allude to an affective component to social bonds. For example, social relationships are thought to vary based on tenor and tension (Silk et al. 2013). By synthesizing the different components of relationships (Hinde 1987; Silk et al. 2013), I identify two main axes to categorize social relationships: the endurance of a relationship and whether it is characterized by positive of negative affect (Figure 2). But few studies of primate behavior examine these affective components. This is despite the common practice of classifying behaviors as "affiliative" and "agonistic," which implies an affective component.

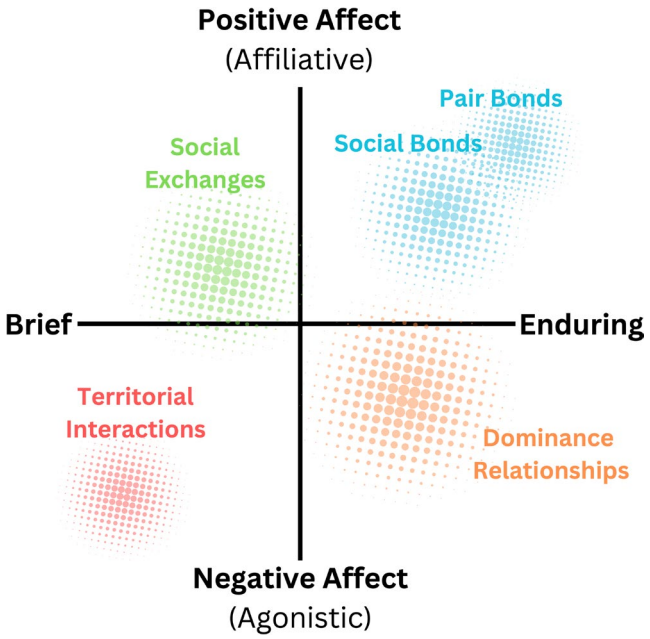

FIGURE 2 | Social relationships can be placed on two main axes. Relationships can range from affiliative to agonistic, which is displayed on the *Y*-axis. Relationships can also range from brief to enduring, which is displayed on the *X*-axis. Social bonds are affiliative and enduring, with pair bonds being even more affiliative and more enduring. Affiliation and agonism include an affective component, although scientists studying relationships in animals rarely quantify this and instead make tacit interpretations about whether the behavior is high/low arousal and is positive or negative.

4 | Prioritizing Description for a New Science of Emotions

A paradigm for understanding and quantifying emotions is crucial if we want to make progress toward understanding the range of relationships that occur in humans and other animals, especially if we are to attempt a scientific study of love. Importantly, we need to quantify the emotions or affective states that we typically consider as pleasure, attraction, and intimacy (e.g., Cunningham and Benítez 2024). In this regard, we should reinvest efforts in detailed description to accurately characterize the phenomena under consideration. "We must hope that the descriptive phase is not going to come to a premature ending." Tinbergen wrote in 1963. "Already there are signs that we are moving into an analytical phase." I advocate a return to description and doing so with new tools which allow a detail hitherto unavailable.

Behavioral ecologists and ethologists have long emphasized the importance of recording only what is visible, with operational definitions of behavior based on movements, not projections of what the animal might be thinking or feeling. The desire to avoid anthropomorphizing our study subjects is a valid concern, especially given the conceptual difficulties with defining emotions across species, which confounds attempts to study affective states. A long history from philosophy, psychology, and early

ethology argued that non-human animals lack emotions (de Waal and Andrews 2022). This view is changing due to the efforts of primatologists who study empathy, cooperation, and cognition (de Waal 2011; Kret et al. 2020; Rogers and Bales 2022; Heesen et al. 2024). There is also a growing focus in neuroscience on the psychophysiology of affective states in rodents (Panksepp and Lahvis 2011; Zych and Gogolla 2021; Shemesh and Chen 2023).

Emotions and their correlates may be visible to the careful observer, and primatologists should turn their attention to this possibility to strengthen our ability to describe social bonds. We need to integrate the theory and methods used by field primatologists and other animal behavior researchers with those of psychologists and neuroscientists (Battivelli et al. 2024). Some basic frameworks could be useful, like core affect theory, which models emotions as varying across two main dimensions: high to low physiological arousal on one axis and positive to negative valence on the other axis (Russell 2003). Novel methods for describing subtle aspects of behavior and physiology will open new possibilities for understanding relationships in animals, including humans. Advances in computer vision and machine learning allow fine-grained analysis of behavior and affective states (Marks et al. 2022; Bordes et al. 2023; Vogg et al. 2024). Such methods are often limited to rodents in lab settings (Dolensek et al. 2020). Some of these methods have also been applied to primates in captivity and the wild, including facial recognition (Schofield et al. 2023; Paulet et al. 2024) and "pose estimation" to record posture and movement (Desai et al. 2023; Wiltshire et al. 2023). These machine learning techniques, which identify subtle aspects of gaze and movement, can be broadened to infer bodily movements and expressions that signify affect. For example, what are the movements and micro-movements that occur during grooming long-term vs. short-term partners, or between mothers and their offspring compared to adult females and other similarly aged group members? By using key-point tracking and pose-estimation software, it is possible to quantify posture and movement in two-dimensional space using model-reductions. Species can be distinguished based on their posture (e.g., Desai et al. 2023). Perhaps the micro-postures of different affective states or relationships can be distinguished as well.

Just as microscopes allowed us to identify the microstructure of anatomy, high-quality videos combined with machine learning technologies will allow us to see the microstructure of behavior. As we develop and implement these new tools, we should move away from using broad placeholders for behavior, such as "grooming," and instead quantify different types of grooming, which may reflect different types of relationships (e.g., Hikida 2022; Schino et al. 2023). In the grooming that occurs between chimpanzees (Figure 3), might we be able to distinguish among alliances, short-term social exchanges, and emotionally charged social bonds (including the strongest relationships which may be better understood as pair bonds)? More detailed descriptions of behavior represent a useful return to early ethology, including when scientists appreciated the qualitative nature of behavior and developed their own ethograms based on direct observation and reflection. Importantly, we should quantify physiological changes that occur alongside different behaviors as well as subtle changes in facial and bodily expressions (e.g., Hikida 2022). Through this more detailed approach, we will be able to provide quantitative measures of attraction and arousal.

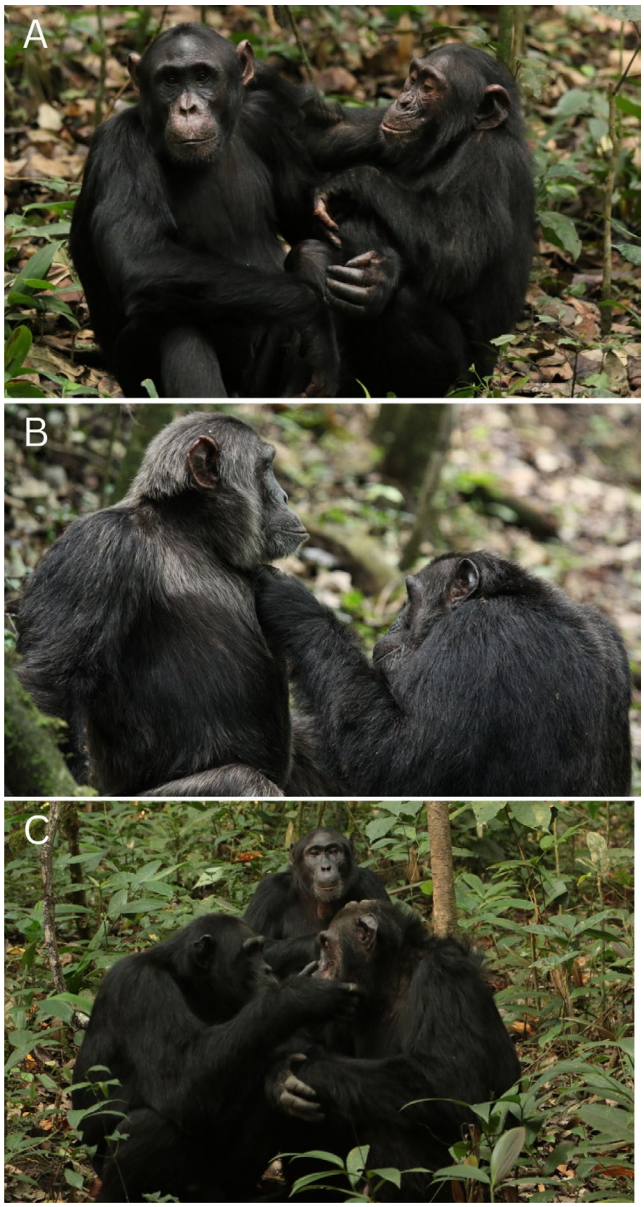

FIGURE 3 | Chimpanzees exhibit strong and enduring grooming relationships. Many of these occur between unrelated adult males. (a) Two adolescent male chimpanzees groom; (b) two high-ranking males groom, which could suggest a "social bond" or an enduring alliance of utility; (c) two adult males, who have a very enduring relationship, groom. The younger brother of the male on the left looks at them several meters away.

This return to description should be informed by research questions and hypotheses, but we should be cautious of how hypotheses bias what we actually see and how we interpret data. It is possible that starting with adaptive hypotheses and trying to test them may lead us astray. Biological anthropologists and primatologists tend to focus on ultimate explanations for human variation and behavioral patterns. Natural selection is the unifying principle of biological anthropology, animal behavior, and other biological disciplines. But we should not necessarily prioritize adaptive hypotheses in our research programs and papers. Providing narratives for the evolutionary history of certain traits is interesting to wide audiences, but we should be cautious in doing so. First, we rarely have the data necessary to test evolutionary hypotheses for

behavior because evolutionary processes unfold across deep space and time. Reproductive success may be the gold standard for quantifying evolutionary fitness in animal behavior, but it may be fools' gold. This is especially the case for long-lived species with slow life histories, like primates. An accurate study of fitness would require identifying the genetic basis of a phenotype and seeing how it proliferates in the population on an evolutionary time scale. For primates, at least, who have long and slow life histories, even the longest studies of reproductive success may be weak proxies for evolutionary fitness. Second, adaptive hypotheses are often veiled projections of our own biases or worldviews, and we should be aware of the social and cultural forces shaping these perspectives (e.g., Kissel 2020; Fuentes 2022) (Box 2).

5 | Relationships in Our Lives and in the Lives of Other Animals

As biological anthropologists seek to understand love and social bonds across species, it is important to appreciate that humans are a valuable resource. We are apes. Yes, we are complicated by cultural variation, inhibition, and repression. But so much of our behavior and psychology has its foundation in the fact that we are apes and primates and mammals. We can leverage this fact to develop better metrics for understanding emotions in other species. Research into relationships and the underlying behavior and emotions should draw on studies of humans and other animals, both in experimental settings as well as in the wild. For example, we can pair psychophysiological data and bodily expressions in humans in different contexts (e.g., varying relationship type, mood, etc.). And we can interview those people about their experience to provide a "ground truth" for the observational metrics indicative of emotions.

We can also draw inspiration from the variable ways in which people theorize about love and practice loving relationships. The current, dominant models of relationships, sexuality, gender, and family may not accurately represent the human experience. In this regard, the well-trained scientist should not only describe "what is," but "what is possible." How does love, desire, intimacy, and friendship manifest in various contexts—across a variety of cultures and identity groups? For a scientific study of love and loving relationships, hypotheses arising from our own experiences and drawn from a range of disciplines, from literary criticism to queer theory, are especially valuable (e.g., Sedgwick 1985; Carter 2005; Schippers 2016; Halperin 2019). Without such perspectives, we may overlook or misinterpret important relationships in our own lives.

By expanding our perspectives as scientists, we will be better positioned to accurately see and study relationships in other species. In this way, we can use humans to better understand our fellow primates, and then use our comparative study of primates to, in return, elucidate the human experience. Today, so many societies are grappling with crises of loneliness, polarization, and violent conflict. Part of the problem is that we do not fully understand the social bonds that hold us together, and we do not prioritize enough the ties of friendship and community. We are in need of new theories and practices about love.

BOX 2 | Attention to bias and bigotry.

We should be cautious about proposing hypotheses about the adaptive (or maladaptive) aspect of relationships and behavior. For example, many scholars offer evolutionary explanations for homosexual behavior in humans (Kirkpatrick 2000; Monk et al. 2019; Barron and Hare 2020; Gómez et al. 2023). Sometimes these hypotheses are creative and arise out of a commitment to normalizing various sexualities in humans today. But we rarely have the data necessary to test adaptive hypotheses for behavioral phenomena. We also need to identify how ideas based on recent history, current politics, movies, and social norms—contemporary myths and narratives—creep into our scientific outlooks (Fuentes 2022; Simha et al. 2024). Many "folk ideas" offer important insights. Other ideas may arise from bigoted or normative bases, and those can have a harmful impact. For example, anti-LGBTQ+ sentiments and policies prevailed in the United States for much of the 20th century. Same-sex marriage was illegal in most of the United States until a 2015 Supreme Court ruling found such bans unconstitutional. And only in 2020 did a Supreme Court ruling add workplace protections for people based on their gender and sexual identity. This culture of discrimination may be reflected in our hypotheses about social and sexual behavior in humans and other animals. Even less harmful norms, like the prioritization of marriage, with its economic and policy implications, likely skews how we interpret animal behavior, including our own. Our science will benefit by expanding our personal and academic understanding of what relationships are possible and pleasurable in humans and other organisms (e.g., Weiner and Young 2011; Schippers 2016; Katz and Katz 2022).

Author Contributions

Aaron A. Sandel: conceptualization (lead), writing – original draft (lead), writing – review and editing (lead).

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Conflicts of Interest

The author declares no conflicts of interest.

Data Availability Statement

No datasets were generated or analyzed during the current study.

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