The expression of empathy in human's closest relatives, bonobos and chimpanzees: current and future directions

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ABSTRACT

Empathy is a complex, multi-dimensional capacity that facilitates the sharing and understanding of others' emotions. As our closest living relatives, bonobos (*Pan paniscus*) and chimpanzees (*P. troglodytes*) provide an opportunity to explore the origins of hominin social cognition, including empathy. Despite certain assumptions that bonobos and chimpanzees may differ empathically, these species appear to overlap considerably in certain socio-emotional responses related to empathy. However, few studies have systematically tested for species variation in *Pan* empathic or socio-emotional tendencies. To address this, we synthesise the growing literature on *Pan* empathy to inform our understanding of the selection pressures that may underlie the evolution of hominin empathy, and its expression in our last common ancestor. As bonobos and chimpanzees show overlaps in their expression of complex socio-emotional phenomena such as empathy, we propose that group comparisons may be as or more meaningful than species comparisons when it comes to understanding the evolutionary pressures for such behaviour. Furthermore, key differences, such as how humans and *Pan* communicate, appear to distinguish how we experience empathy compared to our closest living relatives.

Key words: empathy, *Pan*, bonobo, chimpanzee, consolation, contagion, mimicry, targeted helping, perspective-taking.

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I. INTRODUCTION

Empathy is a socio-emotional capacity that involves recognising and being emotionally influenced by the emotions of others, enabling corresponding prosocial responses and cooperative behaviour (Preston & de Waal, 2002). Despite definitional inconsistencies, most scholars characterise empathy as an automatic, affective response to emotional stimuli, shaped by top-down control processes, which may trigger a prosocial behavioural response (Cuff *et al.*, 2016). Empathy is thus important for developing and maintaining strong, long-term cooperative relationships among social animals (Rumble, Lange & Parks, 2010).

A leading model to describe empathy is the Perception–Action Model (PAM; Preston & de Waal, 2002). According to the PAM, empathic processes arise from perceiving another's external state or action. This evokes representations of such states or actions in oneself, which then result in a corresponding response. Relatedly, the Russian Doll Model of empathy describes this perception–action pairing as the core mechanism that facilitates more other-oriented behaviours, including targeted helping and sympathetic concern (de Waal, 2007). Alternatively, Yamamoto (2017) has proposed a similar but non-linear componential conceptualisation where separate factors – namely, matching other's states, understanding other's states, and prosociality – overlap in various combinations to produce empathy-related behaviours. Critically, regardless of linearity, behavioural research suggests that various social mammals, and primates in particular, are capable of all of these layers, or components, of empathy (Adriaense *et al.*, 2020; Brooker, Webb & Clay, 2022).

Affective states can spread from one individual to another spontaneously and consciously, yet various factors can mediate the expression of empathy. Experiencing the suffering of others indiscriminately would likely not be advantageous if it depletes one's own socio-emotional resources or puts them at risk. The empathy mechanism appears to be influenced by individual and social factors such as an empathy gradient, which has been identified in humans and some non-human species (Fraser, Stahl & Aureli, 2008; Palagi & Norscia, 2013; Lindegaard *et al.*, 2017). This gradient alludes to a heightened emotional representation of another's state if they have a strong relationship with oneself, such as close social partners or kin (de Waal, 2012; de Waal & Preston, 2017). This trend offers a selective explanation as to how a potentially costly behaviour may have emerged among social animals. Primates thus provide suitable models for study here, as most species, especially apes, invest in long-term social cooperative relationships with kin and other group members throughout their lifetimes.

In recent decades, scientific discoveries have uncovered social and cognitive capacities, such as culture – the possession and transmission of socially learned traditions, characteristic of particular groups of conspecifics (Whiten *et al.*, 1999) – in other animals that were once thought to be unique to humans (Whiten & van Schaik, 2007). In the case of empathy, inconsistencies in defining and operationalising empathy in empirical research (Cuff *et al.*, 2016), and a lack of systematic comparative designs, have limited direct between-species comparisons, which are needed to identify the breadth of empathy in animals. Despite these hurdles, our closest living primate relatives – the *Pan* apes, bonobos (*Pan paniscus*) and chimpanzees (*Pan troglodytes*) – provide suitable models for testing open questions about the ancestral roots of empathy and social cognition. Comparative research on great apes helps us uncover clues about what types of social behaviours our last common ancestor with *Pan* may have exhibited. In addition, whereas *Pan* overlap with each other and humans in many aspects of their social dynamics and behaviour, these species provide a further window into how variations in social structures may foster changes in expressions of phenomena like empathy. In this review, we outline current insights into understanding empathic behaviour in *Pan* with some proposed new directions, that can provide a more nuanced and broader view about animal empathy. As cross-species investigations are vital for revealing how human empathy may have evolved, we also advocate the rationale for more systematic comparisons of the two species.

II. *PAN* SIMILARITIES AND DISTINCTIONS

Like most primate species, bonobo and chimpanzee societies are characterised by long-term social bonds among group members. However, unlike most primate species, the males of both *Pan* species are the philopatric sex, with females typically emigrating at sexual maturity (Gruber & Clay, 2016). Both species live in large multi-male, multi-female fission–fusion societies, with subgroupings that vary in membership over time (Boesch, Hohmann & Marchant, 2002). While male philopatry predicts males to be the most socially bonded sex, among *Pan* this pattern is only expressed in chimpanzees. Whilst relationship quality can vary among females across populations and ecological conditions (e.g. Wakefield, 2008, 2013), male chimpanzees tend to exhibit the strongest social bonds and occupy the highest status positions (Goodall, 1986; Boesch *et al.*, 2002). By contrast, bonobo societies are characterised by female–female and mixed-sex bonding, with dominance hierarchies that are typically female-centric (Boesch *et al.*, 2002). Male–male alliances in chimpanzees and female–female alliances in bonobos between dominant individuals are crucial for their

respective intragroup social stability (Gruber & Clay, 2016). Given this striking variation in bonding and hierarchical structure between *Pan* species, one might expect sex-biased variation in socio-emotional tendencies between the two species, including empathy.

Compared to chimpanzees, bonobos are less aggressive (Wilson *et al.*, 2014) and have been considered to be the more empathic species – the 'make love not war' ape (de Waal & Lanting, 1997) that uses sexual behaviour to resolve social conflicts (Hohmann & Fruth, 2000). Whilst they also engage in aggression (Fruth & Hohmann, 2003; Hare, Wobber & Wrangham, 2012), bonobo societies are regularly described as having a more peaceful nature (Furuichi, 2011) with lower inter- and intragroup aggression levels than those described for chimpanzees (Hare *et al.*, 2012). Bonobos also appear to be relatively tolerant of other groups, having been observed peacefully interacting with neighbouring groups at artificial and natural feeding locations (Idani, 1990; Sakamaki *et al.*, 2018; Lucchesi *et al.*, 2020a). Furthermore, no observation of intra-species killing has yet been confirmed for bonobos (Furuichi, 2011; Wilson *et al.*, 2014).

By comparison, chimpanzees are depicted as more aggressive, with much empirical focus on their patriarchal hierarchies and antagonistic interactions within and between groups (de Waal, 2005). Intergroup competition is a ubiquitous feature among chimpanzee communities and encounters are often hostile with threat vocalisations and or physical aggression likely to occur (Wilson & Wrangham, 2003). Chimpanzees have been documented killing group and non-group members (Boesch *et al.*, 2007; Pruetz *et al.*, 2017), with their behaviour explained as strategic and adaptive responses to competition over territory, resources, and mating opportunities (Williams *et al.*, 2004). In addition, whilst social bonding is key to chimpanzee nature, bonobos have been reported as more socially attentive than their *Pan* counterparts (Kano, Hirata & Call, 2015).

Despite these differences, bonobos and chimpanzees appear to overlap more in terms of social tolerance than previously thought (Cronin, de Groot & Stevens, 2015; van Leeuwen *et al.*, 2023). Previously, bonobos had commonly been considered the more tolerant species due to their lower aggressivity, their potential to coalesce with other groups, and their rapid responsiveness towards others' emotional expressions (Kret *et al.*, 2016). However, a recent study of cofeeding tolerance in zoo- and sanctuary-living populations revealed greater variation within the two species than between them (van Leeuwen *et al.*, 2023).

In bonobo societies, the prevalence of non-conceptive sexual behaviour, which occurs among all age and sex combinations (de Waal, 1990; Hohmann & Fruth, 2000), is thought to facilitate cooperation and reduce aggression compared to chimpanzees (de Waal, 1995; Clay & de Waal, 2015). However, chimpanzees also engage in genital contacts, with observations from both the wild and captivity (Anestis, 2004; Zamma & Fujita, 2004; Sandel & Reddy, 2021). In both species, sexual contacts are particularly common during periods of social tension, indicating a shared strategy of

tension management through sexual interactions (Clay & de Waal, 2015; Sandel & Reddy, 2021).

Here we review the literature on the different components of empathy in *Pan*. Chimpanzees feature more prominently, due to a study bias towards chimpanzees in empirical socio-cognition studies (Clay *et al.*, 2022). Bonobos and chimpanzees appear to have certain marked species differences in behaviours that may influence empathic expressions, such as socio-emotional attentiveness. However, we propose that marked within-species variation, behavioural flexibility, and the possible existence of variable social cultures are of greater interest than direct species differences between bonobos and chimpanzees. We offer some proposed future directions that may provide a more nuanced and broader way of thinking about *Pan* empathy and its relevance to understanding how empathy has evolved.

III. STUDYING EMPATHY IN *PAN*

(1) Mimicry and behavioural contagion

Emotional responses can occur automatically (Lamm, Batson & Decety, 2007), as seen in some observations of mimicry and contagion in human and non-human animals. Mimicry, both rapid (i.e. within 1 s) and delayed (i.e. between 1 and 5 s), is considered the copying of the physical appearance of others, for example by replicating facial expressions or vocalisations (Chartrand & Bargh, 1999; Zentall, 2003). Mimicry has been observed in a diverse array of species, across various levels of sociality and cognitive capacity, and in various contexts (Kret & Akyüz, 2022). Similarly, humans and other primates also appear to engage in behavioural contagion, considered the spread of self-directed or social motor actions such as auto- or allogrooming (Amici, Aureli & Call, 2014a). Whilst some examples of delayed mimicry or behavioural contagion could imply conscious application (Palagi *et al.*, 2019), both mimicry and contagion are broadly assumed to be involuntary and reflexive. In this review, we describe mimicry and behavioural contagion together, as manifestations of the most basal empathic mechanisms that facilitate more complex behaviours.

Mimicry and behavioural contagion have been studied in humans (Norscia & Palagi, 2011b), as well as in captive and semi-wild *Pan* populations (Madsen *et al.*, 2013; Tan, Ariely & Hare, 2017). A number of studies have proposed links between mimicry, empathy, and emotion contagion (Adriaense *et al.*, 2020). It remains unclear whether, and to what extent, mimicry and corresponding internal states are directly linked, in humans and other animals alike (Adriaense *et al.*, 2020). Evidence of a specific physiological or behavioural response would be needed to support an association with these phenomena (Isern-Mas & Gomila, 2019). Yet, as a building block towards perspective-taking abilities, reflexive state-matching behaviours may have been favoured, due to influences in social bonding

(Seyfarth & Cheney, 2013). This may assist immature individuals in learning the correct contexts and usage for social behaviours and in forming affiliative relationships (Want & Harris, 2002). Mimicry and behavioural contagion could thus contribute to the foundations of empathic expressions due to their involvement in affiliative bonding.

When responding empathically, we may unconsciously merge the self and other, thereby echoing another's experiences within ourselves (de Waal, 2011). The Russian Doll model proposes that mimicry acts as a prerequisite for more complex socio-emotional behaviours (de Waal, 2007; de Waal & Preston, 2017), which may explain why facial mimicry is a common reflex after observing emotional expressions. Looking at facial muscle movements, Dimberg & Thunberg (2012) found that human participants mimicked happy and angry faces and reported experiencing the equivalent emotion even when stimuli were presented to them too quickly for conscious perception.

Similar to the neonatal human studies by Meltzoff & Moore (1977), (but see Davis *et al.*, 2021), small samples of captive neonatal chimpanzees appeared to attend to social stimuli and mimicked model facial expressions (Myowa, 1996; Bard, 2007). Even newborn chimpanzees appeared to copy and discriminate the basic facial expressions from human models (Myowa-Yamakoshi *et al.*, 2004), although such work requires further replication with larger samples. This mimicry process generally stops after 2 months, indicating that this behaviour is possibly an adaptive reflex. In addition, a study of social behavioural contagion in captive chimpanzees (Videan *et al.*, 2005) found that hearing grooming and aggressive vocalisations from an outgroup triggered individuals to reproduce these respective behaviours in their own group. These responses could be stimulated by feelings of intergroup threat, but they may also be driven by similar mechanisms to other behaviour and emotion contagion effects, such as those that facilitate yawn contagion and physiological state matching.

Whilst these behaviours may not reflect a full empathic response, there is a strong correlative link between mimicry and behavioural contagion with emotional contagion (Palagi *et al.*, 2020b). This motor contagion is purported to have served as an exaptation for emotional contagion when viewing the emotional internal states of others, such as facial expressions (Hess & Fischer, 2013). Thus, mimicry and behavioural contagion may facilitate the outer layers of empathy, as per the Russian Doll model (de Waal, 2007), by representing contagion of a similar emotional state (Palagi *et al.*, 2020b). In support, the PAM posits a close link between perceiving and performing actions in the brain: the mirror neuron system – a neural network integral to this model – fires both when an individual performs an action and when they observe the same action in others (Gallese & Goldman, 1998; Preston & de Waal, 2002). Furthermore, Palagi *et al.* (2020b) suggest that mimicry and behavioural contagion may inform emotional contagion, as opposed to merely creating synchrony. Responses such as yawn contagion may be biased by the same influences that mediate emotional contagion unevenly across humans and apes, such as age and social relationship (Bartholomew & Cirulli, 2014; Campbell & de Waal, 2011; Demuru & Palagi, 2012). As such, we now discuss findings in *Pan* regarding more specific study areas on mimicry and behavioural contagion: rapid and delayed facial mimicry, and yawn contagion.

(a) Rapid and delayed facial mimicry

Primate mimicry research has generally focused on the play-face, which is considered homologous to the human smile and facial laughter and appears to evoke positive affective states in the perceiver (Davila-Ross & Dezecache, 2021; Parr & Waller, 2006). The play-face may reveal internal positive affect and/or non-aggressive intentions in the performer that can be interpreted rapidly and accurately by observers, potentially triggering matching conspecific reactions. Play-face mimicry may therefore have adapted to convey honest intentions of positive interactions, reducing the risk of misunderstandings and conflict (Palagi, 2008). Chimpanzees have been observed to display both rapid facial mimicry (RFM; occurring within 1 s) and delayed facial mimicry (DFM; within 5 s), with each seeming to serve separate functions (Palagi *et al.*, 2019). Palagi *et al.* suggested that RFM helps to prolong play sessions and communicate a playful motivation, whilst DFM modulates sessions at later stages.

In bonobos, RFM and DFM of play-faces has been demonstrated in infants (Bertini *et al.*, 2022). Both forms of play-face mimicry did not appear to influence play session length but were both enhanced by face-to-face contact. Thus, Bertini *et al.* (2022) suggest that, as bonobo play sessions may be relatively balanced, these responses signal reciprocal playful moods between the interacting pairs. Furthermore, RFM of the silent-bared-teeth expression has been observed during sexual encounters. Among captive bonobos in Wilhelma Zoo, the duration of sexual contacts appeared to increase when homo- and heterosexual partners rapidly mimicked the silent bared-teeth facial expression, particularly among female–female dyads (Palagi *et al.*, 2020a). Therefore, by prolonging such interactions, facial mimicry in a sexual context may help to develop social relationships and, in the case of heterosexual dyads, increase the likelihood of conception.

(b) Yawn contagion

Yawn contagion, where one individual yawns in a relaxed or experimental context and triggers a matched response in the observer (Massen & Gallup, 2017), is the most prevalent approach to studying facial mimicry and contagion in humans and other species. Although yawning itself appears to have physiological and social functions (Gallup, 2011), the contagion of yawning seems to be a social phenomenon associated with emotional affinity and social responsiveness (Norscia & Palagi, 2011b; Norscia *et al.*, 2020). In humans, even just thinking or reading about yawning can trigger contagion (Provine, 1986). Neuroscientific research has found that viewing a yawn activates neural regions associated with

self-processing and theory of mind (Massen & Gallup, 2017). This may explain why yawn contagion is more prevalent among human participants with higher perspective-taking skills and lower recorded schizotypal traits (Platek *et al.*, 2003). Types of behavioural contagion therefore could be associated with other-oriented processes.

A comparative study of the four non-human great apes showed that, when exposed to various voluntary and involuntary motor actions, only chimpanzees showed response facilitation, and only when exposed to yawning (Amici *et al.*, 2014*a*). Moreover, this effect was only present when the model stimulus was a conspecific. However, other studies have demonstrated both *Pan* species responding contagiously to conspecifics yawning through experimental (Campbell *et al.*, 2009; Palagi, Norscia & Demuru, 2014*b*) and non-experimental means in captive groups (Demuru & Palagi, 2012; Campbell & Cox, 2019).

Like humans, *Pan* yawn contagion may be enhanced by social closeness (Demuru & Palagi, 2012; Palagi *et al.*, 2014*b*). As previously discussed, empathy tends to be biased towards kin and close social partners (de Waal, 2008; Tan *et al.*, 2017). Thus, some scholars have considered that contagion phenomena and their association with the PAM and mirror neuron system may reflect a wider link to an individual's empathic tendencies, while others remain sceptical (Massen & Gallup, 2017). Meanwhile, other reports have found no social bias in contagion response for chimpanzees (Massen, Vermunt & Sterck, 2012; Madsen *et al.*, 2013) and human children (Cordoni, Favilli & Palagi, 2021), indicating that the link between yawn contagion and empathy may not be as clear cut as once thought and may be influenced by age (Massen & Gallup, 2017). In chimpanzees, this social bias appears to be limited to ingroup/outgroup membership, whereby within-group social relationships do not influence the contagion effect, but outgroup conspecific models do not trigger contagion (Anderson, Myowa-Yamakoshi & Matsuzawa, 2004; Campbell & de Waal, 2011, 2014; Massen *et al.*, 2012; Madsen *et al.*, 2013). In addition, other bonobo studies have revealed a lack of social bias in yawn contagion responses (Norscia *et al.*, 2022), and some sanctuary-living individuals even respond to strangers (Tan *et al.*, 2017). These findings have been purported to reflect the apparent xenophilic nature of bonobos.

There also appears to be an effect of sex interacting with species. In chimpanzees, the yawns of male chimpanzees are more contagious than those of females (Massen *et al.*, 2012); whereas the opposite is the case for bonobos (Demuru & Palagi, 2012). This may be due to differences in social attention biases between the two species, with males more socially central and dominant in chimpanzee groups and females taking this role in bonobo groups (Boesch *et al.*, 2002). Interestingly, whilst human research suggests empathy increases with age (Oh *et al.*, 2020), yawn contagion effects are strongest in young individuals and decrease linearly with age (Bartholomew & Cirulli, 2014). Conversely, whilst age effects have not been observed in zoo-living bonobos (Demuru & Palagi, 2012), yawn contagion was not observed in infant sanctuary-living chimpanzees (Madsen *et al.*, 2013). However, this may be

unsurprising, given that yawn contagion only seems to emerge in human infants around 3 years of age (Cordoni *et al.*, 2021). Whilst we must consider alternative explanations for why contagious yawning may be recorded – such as coinciding stress relief or boredom (Adriaense *et al.*, 2020) – if yawn contagion truly reflects emotional contagion, this phenomenon would support previous claims of automatic mimicry having adaptive origins. A summary of studies testing the presence of various forms of mimicry and behavioural contagion in bonobos and chimpanzees is provided in Table 1.

(2) Emotional contagion

Emotional contagion refers to what occurs when one individual matches with another individual's emotional state, triggering similar states in oneself (Hatfield, Cacioppo & Rapson, 1993). Emotional contagion is thought to foster emotional synchrony between individuals (Hatfield *et al.*, 1993). Cortisol and alpha-amylase – salivary hormones associated with internal stress – appear to increase in humans observing conspecifics engaged in stress-inducing tasks (Buchanan *et al.*, 2012). These increases were associated with self-reported empathic concern and perspective-taking abilities, indicating that affective state-matching may be associated with appraisal of others' situations.

Detecting emotion is difficult in any species. Recent innovative methods to explore how physiological states change in response to emotional stimuli have indicated the existence of emotional contagion in humans and other animals. One such physiological approach is pupil mimicry, the automatic and unconscious synchronisation of pupil size between two individuals in response to emotional or social cues (Bradley *et al.*, 2008). Whilst the relationship of pupil mimicry to emotional contagion is under debate (Derksen *et al.*, 2018), effects are stronger between close social partners (Kret, Fischer & De Dreu, 2015), indicating that pupil mimicry may be associated with social bonding and emotional engagement. Humans and chimpanzees have both been shown to mimic the pupillary dilation of conspecifics (Kret, Tomonaga & Matsuzawa, 2014), and this has been associated with increased attention, arousal, and activation of brain regions associated with social engagement and the theory-of-mind network (Prochazkova *et al.*, 2018). Whilst emotional contagion studies usually feature limited sample sizes and effects, these findings indicate that pupil mimicry may facilitate instantaneous communication of internal states, which may provide adaptive benefits of improving the quality of social interactions.

Another technique to monitor physiological reactions is infrared thermography (IRT). This non-contact approach allows detection of activity of the autonomic nervous system in response to affective stimuli (Speakman & Ward, 1998). Studies show that human facial temperatures change in response to socio-emotional situations. A study of maternal response to infant distress suggested that mothers and children affect-match during specific emotional contexts (Ebisch *et al.*, 2012). So far, the core regions of interest for IRT in detecting possible emotional responses include the

Table 1. Compilation of studies investigating mimicry and behavioural contagion in bonobos and chimpanzees. Abbreviations: C = captive; S = sanctuary; '^e' = experimental; '^o' = observational; *pp* = *Pan paniscus*; *pt* = *Pan troglodytes*.

Species	Reference	N	Setting	Evidence of mimicry or behavioural contagion
Pan paniscus, *P. troglodytes*	Amici *et al.* (2014*a*)	*pp* = 4, *pt* = 14	C	Yawn contagion[e]: *pp* = No support; *pt* = Supported Scratching contagion[e]: No support Nose wiping contagion[e]: No support
P. paniscus	Bertini *et al.* (2022)	*pp* = 5	C	Rapid facial mimicry[o] (during play interactions): Supported Delayed facial mimicry[o] (during play interactions): Supported
P. paniscus	Demuru & Palagi (2012)	8	C	Yawn contagion[o]: Supported
P. paniscus	Norscia *et al.* (2022)	18	C	Yawn contagion[o]: Supported
P. paniscus	Palagi *et al.* (2014*b*)	16	C	Yawn contagion[e]: Supported
P. paniscus	Palagi *et al.* (2020*a*)	10	C	Rapid facial mimicry[o] (during sexual interactions): Supported
P. paniscus	Tan *et al.* (2017)	25	S	Yawn contagion[e]: Supported
P. troglodytes	Anderson *et al.* (2004)	6	C	Yawn contagion[e]: Limited support (2/6 subjects exhibited contagion)
P. troglodytes	Bard (2007)	5	C	Neonatal facial mimicry[e]: Supported
P. troglodytes	Campbell *et al.* (2009)	24	C	Yawn contagion[e]: Supported
P. troglodytes	Campbell & Cox (2019)	18	C	Yawn contagion[o]: Supported
P. troglodytes	Campbell & de Waal (2011)	23	C	Yawn contagion[e]: Supported
P. troglodytes	Campbell & de Waal (2014)	19	C	Yawn contagion[e]: Supported
P. troglodytes	Madsen *et al.* (2013)	33	S	Yawn contagion[e]: Supported
P. troglodytes	Massen *et al.* (2012)	15	C	Yawn contagion[e]: Supported
P. troglodytes	Myowa (1996)	1	C	Neonatal facial mimicry[e]: Supported
P. troglodytes	Myowa-Yamakoshi *et al.* (2004)	2	C	Neonatal facial mimicry[e]: Supported
P. troglodytes	Palagi *et al.* (2019)	15	C	Rapid facial mimicry[o] (during play interactions): Supported Delayed facial mimicry[o] (during play interactions): Supported
P. troglodytes	Videan *et al.* (2005)	51	C	Affiliative behavioural contagion[o]: Supported Aggressive behavioural contagion[o]: Supported Vocal contagion[o]: Supported

nasal, perinasal, orbital, periorbital, and maxillary regions of the face (Ioannou, Gallese & Merla, 2014). Reductions in nasal and maxillary area temperatures have been associated with exposure to upsetting social contexts and other negatively valenced stimuli (Ioannou *et al.*, 2013, 2016).

Dezecache *et al.* (2017) found significant changes in the ear and nose surface temperatures of wild chimpanzees in response to naturally occurring conspecific vocalisations. Aversive calls, such as aggressive barks, were associated with the largest changes in nasal temperatures (Dezecache *et al.*, 2017). In captivity, nasal tip temperatures in chimpanzees decreased significantly in response to playbacks of conspecific agonism (Kano *et al.*, 2016). Further activation of the sympathetic nervous system was noted, as heart-rate variability and behavioural arousal also occurred (Kano *et al.*, 2016). Other video playback experiments have revealed vicarious responses in chimpanzee viewers, whereby emotional images appeared to trigger decreased skin temperatures and increased tympanic membrane temperatures (Parr & Hopkins, 2000; Parr, 2001).

However, other aversive stimuli, such as viewing an injury on a human experimenter, appear to reduce nasal temperature in captive chimpanzees (Sato, Hirata & Kano, 2019). In addition, chimpanzees can distinguish between scream variants that form a graded continuum, being more attentive to severe victim screams than acoustically similar tantrum screams (Slocombe, Townsend & Zuberbühler, 2009). Therefore, contextual cues and further control conditions are needed to make it possible to rule out arousal responses to aversive events that may be unrelated to the conspecific's state, and more to one's own personal negative experiences. Applying non-invasive arousal-detection techniques alongside behavioural experiments may make it possible to detect whether social responses to emotional stimuli are associated with underlying affective state-matching responses. A summary of the literature investigating physiological changes in response to potential emotion-inducing stimuli in chimpanzees and possible cases of emotional contagion is provided in Table 2.

(3) Consolation

While detecting the underlying mechanisms of empathy requires careful experimentation and/or physiological markers, some behavioural manifestations of empathy can

Table 2. Compilation of studies investigating physiological changes in response to potential emotion-inducing stimuli in chimpanzees and possible cases of emotional contagion, including key relevant findings. Abbreviations: C = captive; S = sanctuary; W = wild; "e" = experimental; "o" = observational; IRT = infrared thermography.

Species	Reference	$\mathcal{N}$	Setting	Evidence of behaviour
P. troglodytes	Dezecache *et al.* (2017)	14	W	Emotional contagion[o] (IRT): nasal temperature changes during aversive stimuli
P. troglodytes	Kano *et al.* (2016)	12	C, S	Emotional contagion[e] (IRT): nasal temperature decreases in response to conspecific agonism; heart-rate variability and behavioural arousal occurred in tandem
P. troglodytes	Kret *et al.* (2014)	8	C	Pupil mimicry[e]: matched conspecific pupil dilation
P. troglodytes	Parr (2001)	3	C	Emotional contagion[e] (IRT): peripheral skin temperature decreases in response to aversive stimuli; higher towards injection stimuli compared to conspecific agonism; subjects also matched emotional stimuli to facial expressions
P. troglodytes	Parr & Hopkins (2000)	6	C	Emotional contagion[e] (IRT): emotional images appeared to trigger increased tympanic membrane temperatures

be observed by watching how individuals respond to conspecifics in distress. One such behaviour is consolation, which refers to bystanders offering friendly contact to someone in distress, which is effective in reducing the recipient's distress (Zahn-Waxler *et al.*, 1992; Romero & de Waal, 2010). de Waal & Yoshihara (1983) developed the post-conflict/matched-control (PC/MC) method during early studies of zoo-living rhesus macaques (*Macaca mulatta*) to test if bystander-initiated affiliation was more common towards certain individuals during a standardised post-conflict period compared to a matched control recorded at a similar time in the following days. It is suggested that consolation requires the ability to be emotionally affected by, understand, and respond to another's emotion (de Waal & Preston, 2017). Consolation has thus been equated with sympathetic concern as it appears to represent an other-oriented prosocial motivational response to improve another individual's emotional state (de Waal, 2008).

Although the cognitive complexity of consolation remains under debate, genuine consolation (i.e. that which has a tension-reducing function in the receiver and cannot be otherwise clearly explained as having an alternative function) appears to be rare in the animal kingdom, including among primates (Adriaense *et al.*, 2020). Thus far, humans, bonobos, and chimpanzees are three of the few species known to use consolation in their day-to-day social lives (for a review of consolation studies in all animals, see Adriaense *et al.*, 2020). Although ape research is generally limited to captive and semi-wild populations (Fraser *et al.*, 2008; Fraser & Aureli, 2008; Clay & de Waal, 2013; Palagi & Norscia, 2013), wild chimpanzees have been shown to console [Taï National Park, Ivory Coast (Wittig & Boesch, 2003); Mahale Mountains, Tanzania (Kutsukake & Castles, 2004)]. Conversely, consolation has been shown to be absent in an eastern chimpanzee subspecies community at Budongo (Arnold & Whiten, 2001) and in a captive laboratory group (Fuentes *et al.*, 2002). Although wild bonobos have not been explicitly tested, multiple captive and semi-wild bonobo populations have been shown to console (Palagi, Paoli & Tarli, 2004b; Clay & de Waal, 2013). Similar consolation behaviours are seen across *Pan* including embracing, touching, and patting. However, bonobos are much more likely to use sexual contacts to console conspecifics regardless of the age or sex of the victim or consoler (de Waal, 1988; Clay & de Waal, 2015).

In humans, research has generally been limited to developmental studies in young children (Zahn-Waxler *et al.*, 1992; Fujisawa, Kutsukake & Hasegawa, 2006; Roth-Hanania, Davidov & Zahn-Waxler, 2011; Davidov *et al.*, 2013, 2021). However, a recent study showed that adult human consolatory tendencies following robberies resemble those seen in chimpanzee post-conflict studies (Lindegaard *et al.*, 2017). Consolation emerges early in human development, as early as 9 months (Davidov *et al.*, 2013, 2021). Such early responses are also seen in bonobos and chimpanzees, with consistent age effects showing that consolatory tendencies appear to be highest in young individuals and decrease as apes age (Clay & de Waal, 2013; Webb *et al.*, 2017).

Observations of infant humans, apes, and other mammals offering comfort to distressed others contradicts a common assumption that consolation requires complex cognitive processes (de Waal & Preston, 2017). Instead, with age, consolation may become a more conscious and targeted response, whereas in infants it may be more reflexive. Like humans, male chimpanzees have been shown to become more selective in their social interactions as they age, favouring social partners with whom they have a strong reciprocal bond (Rosati *et al.*, 2020). By contrast, younger males appear to be less selective in who they form social bonds with and thus tend to have more one-sided relationships, which become fewer yet more reciprocal as they age. This increasing selectivity may therefore manifest in reduced consolatory tendencies, particularly as recipients of aggression are often younger males and females that older individuals may not have developed a close relationship with (Sabbi *et al.*, 2021). Subsequently, the recipients of these responses may be more

likely to be those with whom the initiator has a stronger reciprocal social bond.

Social closeness has been shown to predict consolation in humans (Lindegaard *et al.*, 2017), bonobos (Clay & de Waal, 2013; Palagi & Norscia, 2013), and chimpanzees (Fraser *et al.*, 2008; Webb *et al.*, 2017). These trends reflect the view that empathic responses are more likely between individuals that share close relationships (Preston & de Waal, 2002). Therefore, empathic behaviours, like consolation, may help to strengthen interpersonal bonds and group cohesiveness. Consolation also appears to be used as a substitute for reconciliation in human children. A developmental study found reconciliation and consolation increased significantly in 5-year-olds, compared to 3- and 4-year-olds, and consolation occurred more often when no reconciliation had taken place (Fujisawa *et al.*, 2006). Consolation may also serve as a substitute for reconciliation in bonobos and chimpanzees (Palagi *et al.*, 2004*b*; Palagi, Cordoni & Tarli, 2006), however other studies have indicated no such function (Clay & de Waal, 2013; Koski & Sterck, 2007). Whilst these differences may be due to methodological or analytical inconsistencies, this between-population variation may also be driven by group differences in the function of consolation.

Sex differences in *Pan* consolation have been suggested but remain unclear. In one study, female chimpanzees seemed to console more than males (Romero, Castellanos & de Waal, 2010). However, other studies have suggested there are no sex differences (Webb *et al.*, 2017). Romero *et al.* (2010) found that despite females appearing to be the most consolatory, high-ranking males actually offered consolation most often. Therefore, it may be likely that structural differences in dominance distribution and social composition across captive groups may facilitate varying tendencies across sex classes. On a similar note, consolation, like other behavioural empathic expressions, is believed to be influenced by levels of social tolerance (de Waal & Aureli, 1996). The presence of consolation in these species indicates that increased tolerance may facilitate empathic responses that might otherwise be inhibited due to intimidation or fear of aggression. This appears to be the case beyond apes, as socially tolerant Tonkean macaques (*Macaca tonkeana*) are another species shown to use true consolation (i.e. bystander-initiated contact affiliation that reduces stress markers in the victim), whereas the despotic Japanese macaques (*Macaca fuscata*) do not (Palagi *et al.*, 2014*a*). Furthermore, higher tolerance towards infants and juveniles in bonobos and chimpanzees, and therefore lower risk of redirected aggression, may explain why consolation is more prevalent in younger age classes.

Consolation enables us to study empathy from a more nuanced perspective; whilst consoling behaviour may be pro-social, motivations may not be strictly altruistic. Victim-directed affiliation may also result in punishment avoidance, social rewards, or personal arousal reduction (Batson, 2010). Consolers may receive benefits through reciprocity, such as receiving post-conflict affiliation in the future (Watts, 2002). Furthermore, consolation may reduce potential reactive aggression in the victim, thereby benefiting the consoler

and the group as a whole (Palagi *et al.*, 2006). Empathy need not be used benevolently; it may be used by humans and other animals for personal or collective fitness benefits that are not necessarily associated with comforting a distressed victim. Consolation is one such behaviour that may be mediated by individual and social factors and not an indiscriminate response brought about by emotional sensitivity. An overview of studies testing the presence of consolation and its stress-reducing function in bonobos and chimpanzees is provided in Table 3.

(4) Perspective-taking

The ability to ascribe mental states to others, known as Theory of Mind (ToM), enables one to take another's perspective (Premack & Woodruff, 1978). ToM can emerge from understanding of what others think and what their actions might be, and knowledge of others' mental states (Goldman, 1989). ToM thereby facilitates the capacity to distinguish between the states of oneself and others, a building block for empathy (Batson, Early & Salvarani, 1997; Decety & Svetlova, 2012). Human studies indicate this ability can increase altruistic motivation – when one is able to imagine how another feels during a period of need (Batson *et al.*, 1997). Cognitive appraisal of another's need thereby enables one to offer targeted assistance to specific needs (de Waal, 2008). However, if perspective-taking goes too far, and one imagines directly being in another's position without clear self–other distinction, personal distress may increase (Batson *et al.*, 1997). Therefore, effective self-regulation of one's own affective state and a distinction between one's own state and that of another is needed for genuine other-oriented concern.

Captive chimpanzees appear capable of understanding the goals of conspecifics (Yamamoto, Humle & Tanaka, 2012) and can process what other individuals can see and not see (Hare *et al.*, 2000; Okamoto-Barth, Call & Tomasello, 2007; Bräuer, Call & Tomasello, 2007). For example, subordinate chimpanzees are able to process what dominant conspecifics perceived during social food problem-solving tasks, including in competitive contexts (Hare *et al.*, 2000; Bräuer *et al.*, 2007). In this experiment, the subordinates preferentially approached food that they knew the dominants had not seen. Subjects even seemed able to keep track of who had seen what, as they consistently chose the hidden options when the dominant individual was replaced with another dominant. This perspective-taking also occurred when the competitors were humans (Hare, Call & Tomasello, 2006). Comparatively, bonobos appear to be more adept than chimpanzees in similar tasks, achieving higher scores in gaze following and tasks on understanding others' goals and intentions (Herrmann *et al.*, 2010).

Therefore, both species appear capable of learning others' visual perspectives and of using this information strategically to navigate social and competitive situations. Chimpanzees also appear to be capable of processing what other individuals can hear. When presented with 'noisy containers' and

Table 3. Compilation of observational studies investigating consolation in bonobos and chimpanzees. Support for presence of triadic affiliation tested through post-conflict/matched-control analysis. Abbreviations: C = captive; S = sanctuary; W = wild; L = laboratory.

Species	Reference	N	Setting	Evidence of consolation	
				Triadic affiliation	Stress-reducing function
P. paniscus	Clay & de Waal (2013)	36	S	Supported	Supported
P. paniscus	Palagi & Norscia (2013)	8–12	C	Supported	Supported
P. paniscus	Palagi *et al.* (2004*b*)	6–11	C	Supported	Not tested
P. troglodytes	Arnold & Whiten (2001)	42	W	No support	Not tested
P. troglodytes	Fraser & Aureli (2008)	22	C	Supported	Not tested
P. troglodytes	Fraser *et al.* (2008)	26–32	C	Supported	Supported
P. troglodytes	Fuentes *et al.* (2002)	5	L	No support	Not tested
P. troglodytes	Koski & Sterck (2007)	30–34	C	Supported	No support
P. troglodytes	Kutsukake & Castles (2004)	18	W	Supported	Not tested
P. troglodytes	Palagi *et al.* (2006)	19	C	Supported	Not tested
P. troglodytes	Romero & de Waal (2010)	32	C	Supported	Not tested
P. troglodytes	Webb *et al.* (2017)	44	C	Supported	Not tested
P. troglodytes	Wittig & Boesch (2003)	∼31	W	Supported	Not tested

'silent containers', both containing desirable food, chimpanzees preferred to search from the silent containers when human experimenters were facing the other way, indicating both a visual and auditory understanding (Melis, Call & Tomasello, 2006). Whilst such research has not yet been conducted with bonobos, one might expect they would be likely to show such capacities, due to their similarities with chimpanzees as well as their other aforementioned documented perspective-taking abilities.

By 9 months of age, human infants can separate the preferences of different agents without generalising (Buresh & Woodward, 2007; Henderson & Woodward, 2012). By 18 months, infants can understand that individuals can have desires and preferences different to one's own (Repacholi & Gopnik, 1997; Ruffman *et al.*, 2018). Explicit false belief understanding, that is being able explicitly to attribute two conflicting views of the world – one's own, aligning with reality, and one that does not – seems to develop from 4 years of age onwards (Baillargeon, Scott & He, 2010; Scott & Baillargeon, 2017). However, a rise in use of non-traditional techniques has uncovered evidence that infants as young as 9 months of age have some capacity for implicit false belief understanding [see Scott & Baillargeon (2017) for a review]. Using eye-tracking techniques, Krupenye *et al.* (2016) found evidence of implicit false-belief understanding in great apes. Bonobos, chimpanzees, and Sumatran orangutans (*Pongo abelii*) showed anticipatory looking to a location where an actor falsely believed an object to be hidden, even though the apes knew it was no longer there.

In summary, humans and *Pan* seem to share a capacity for taking the perspectives of others into account, such as desires and the presence of false beliefs. Humans possess perspective-taking capacities so far not demonstrated in other species, including explicit false-belief understanding (Krupenye, 2021). However, theory-of-mind tests of pre-verbal infants and apes have shown that some forms of perspective-taking

can exist without human language. For apes, many assessments have been conducted in captivity and test responses to experimental stimuli. In the wild, bonobos and chimpanzees navigate their interconnected social worlds seemingly without communication systems that are as complex and multi-faceted as those of humans. For example, chimpanzees coordinate hunts with individuals fulfilling specific roles to ambush and capture prey (Boesch, 1994). Thus, the true extent of how great apes can fully understand the perspectives of others is still unclear. Continued investigation of the most advanced perspective-taking skills in more groups of apes in varying living conditions may yet reveal their presence. A summary of literature investigating perspective-taking in bonobos and chimpanzees is provided in Table 4.

(5) Targeted helping

By accurately discerning another's states and needs, individuals can tailor their active prosocial responses to meet a recipient's specific requirements (de Waal, 2008). This is termed targeted helping (de Waal, 2008), and is thought to require accurate perspective-taking of another individual's situation in order to provide an effective response (Yamamoto *et al.*, 2012). Bonobos' and chimpanzees' helping behaviour has generally been studied experimentally, with variable results including both positive [bonobos (Tan & Hare, 2013; Tan *et al.*, 2017); chimpanzees (Warneken & Tomasello, 2006; Warneken *et al.*, 2007; Yamamoto, Humle & Tanaka, 2009; Yamamoto *et al.*, 2012; Greenberg *et al.*, 2010; Melis *et al.*, 2011; Horner *et al.*, 2011; Crockford *et al.*, 2012; Claidière *et al.*, 2015; Mendonça *et al.*, 2018; Hepach, Benziad & Tomasello, 2019)] and negative or no other-regarding behaviour [bonobos (Amici, Visalberghi & Call, 2014*b*; Tan, Kwetuenda & Hare, 2015); chimpanzees (Silk *et al.*, 2005; Jensen *et al.*, 2006; Vonk *et al.*, 2008; Amici *et al.*, 2014*b*)].

Table 4. Compilation of literature investigating perspective-taking in bonobos and/or chimpanzees, including key relevant findings through experimental paradigms. Abbreviations: C = captive; S = sanctuary; W = wild. *pp, Pan paniscus*; *pt, Pan troglodytes*.

Species	Reference	N	Setting	Evidence of perspective-taking
P. paniscus, *P. troglodytes*	Herrmann *et al.* (2010)	$pp = 34$, $pt = 106$	S	Understanding others' goals/intentions: Supported (bonobos outperformed chimpanzees)
P. paniscus, *P. troglodytes*	Krupenye *et al.* (2016)	$pp = 15$, $pt = 19$	C, S	Implicit false-belief understanding: Supported
P. paniscus, *P. troglodytes*	Okamoto-Barth *et al.* (2007)	$pp = 4$, $pt = 8$	C	Visual perspective-taking (manipulated gaze-following task): Supported (apes followed gaze more when full sight was available)
P. troglodytes	Bräuer *et al.* (2007)	11	C	Visual perspective-taking: Supported (subordinates selected food their dominant competitors could not see)
P. troglodytes	Crockford *et al.* (2012)	33	W	Perspective-taking: Supported (chimpanzees inform ignorant group members of specific threats rather than knowledgeable individuals)
P. troglodytes	Hare *et al.* (2000)	10	C	Visual perspective-taking: Supported (subordinates selected food their dominant competitors could not see)
P. troglodytes	Hare *et al.* (2006)	8	C	Visual perspective-taking: Supported (subjects deceived human competitors by hiding actions in food competition paradigm)
P. troglodytes	Melis *et al.* (2006)	7	C	Visual perspective-taking: Supported (preferred opaque tunnel to clear tunnel for reaching food) Auditory perspective-taking: Supported (preferred silent tunnel to noisy tunnel when reaching food and experimenter facing away)

In a seminal study, Yamamoto *et al.* (2012) found that captive chimpanzees, whilst able to provide targeted help by providing conspecifics with specific tools, generally only helped others when directly requested. Therefore, these responses cannot count as targeted helping as the responses are not spontaneous, despite suggesting an understanding of the needs of others. By contrast, bonobos have been observed voluntarily to aid strangers with obtaining food, even when not overtly solicited (Tan *et al.*, 2017). Furthermore, bonobos have also been seen to share food with unfamiliar conspecifics in return for social interactions, even unselfishly helping strangers reach inaccessible food (Tan & Hare, 2013). In a comparative study, bonobos outperformed chimpanzees on cooperation tasks when food was monopolisable (Hare *et al.*, 2007). Such behaviour may relate to why bonobos appear more willing to interact positively with strangers and build wider social networks.

Distinguishing empathy-related targeted helping from other prosocial responses depends upon whether the action is fine-tuned to an individual's specific situation and needs (Pérez-Manrique & Gomila, 2018). Such flexible behaviours have primarily been reported as case studies and anecdotes in the form of rescuing and epimeletic behaviour, including caring for ill or injured individuals and pre-emptive protection (Pruetz, 2011; de Waal, 2019). There are several qualitative reports of chimpanzees spontaneously affiliating with and helping injured group members (Nishida & Hiraiwa-Hasegawa, 1985; Goodall, 1986; Boesch, 1991). Injury and wound attendance may reflect an understanding of another's suffering and care directed towards an individual and may reflect a motivation to alleviate or ease that suffering. Wound cleaning is a common behaviour in wild chimpanzees, whereby individuals will inspect injuries of conspecifics by licking and grooming them (Nishida & Hiraiwa-Hasegawa, 1985; Goodall, 1986; Boesch, 1991).

Non-human apes have been anecdotally observed to respond to the specific needs of others, such as a young male chimpanzee assisting an unrelated female by carrying her infant (Pruetz, 2011). Neither the female nor infant had expressed any markers of distress, and this behaviour was reported as unusual for this male and did not appear to bring him any direct benefits. Similarly, a group of chimpanzees have been observed to wait for an injured group member who was unable to keep up (Boesch, 1992). In addition, Hirata (2009) has outlined a variety of instances where chimpanzee mothers have rescued infants from dangerous circumstances by observing their behaviour and responding accordingly. There are also case reports in both wild bonobos and chimpanzees where they have helped to remove snares from trapped groupmates [bonobos (Tokuyama *et al.*, 2012); chimpanzees (Amati, Babweteera & Wittig, 2008)].

Furthermore, in bonobos, de Waal (2019) reported an anecdote where a captive dominant male at San Diego Zoo attracted a keeper's attention as some juvenile conspecifics had fallen into a dry moat. The juveniles were unable to get out and if the moat had been filled, they would have drowned due to an inability to swim. Whilst some of these responses may be related to maternal instincts (Hirata, 2009), the notion of providing pre-emptive protection may represent an epimeletic form of targeted helping (Pérez-Manrique & Gomila, 2018), which could reflect a form of empathy; understanding imminent risk and consequences and actively taking prosocial steps to avoid them. These case reports represent instances where individuals may have taken pre-emptive altruistic steps to help others, when the consequences of not helping could have been severe.

It is conceivable to think that our closest living relatives may be able to respond flexibly to the emotional needs of others. Whilst still distantly related to bonobos and chimpanzees, fossil

records indicate that severely injured and disabled Neanderthals were able to survive for relatively long periods, suggesting they were supported by their community (Spikins *et al.*, 2018). Furthermore, the injury or death of fellow group members has been shown to cause observable distress in wild (Boesch, 1991), captive (Anderson, Gillies & Lock, 2010), and semi-wild chimpanzees (van Leeuwen *et al.*, 2016), as seen by vocalisations, agitation, and anxiety-related behaviours. Individuals can be attentive and affiliative towards dying conspecifics and even guard their corpses (Boesch, 1991; Anderson *et al.*, 2010). One case report from sanctuary-living individuals even recorded corpse-cleaning behaviour using tools to remove debris from the teeth of the deceased groupmate (van Leeuwen, Cronin & Haun, 2017*a*). Whilst the individual 'cleaning the corpse' may have been separately motivated to acquire food from the teeth or even to learn about death, the individual notably forfeited high-quality food offered by caretakers in attempts to lure her away from the body. Such care towards injured, weak, and deceased individuals is common in humans and may have ancient evolutionary origins.

It is difficult to measure targeted helping systematically in real-life contexts, such as responding to injuries among humans and *Pan*, due to their rarity. However, experimental studies indicate promising directions for studying empathic responses to others' pain. Human research has shown that observers of painful contexts experience arousal (Hein *et al.*, 2011; Kupfer, 2018), measured as heart rate (Preis & Kroener-Herwig, 2012), pupil diameter (Azevedo *et al.*, 2013) and skin temperature changes (Salazar-López *et al.*, 2015). In human children, prosocial behaviour appears to be motivated by other-oriented concern and inner arousal, as measured in this case by pupil dilation (Hepach, Vaish & Tomasello, 2013). Sato *et al.* (2019) found chimpanzees spontaneously attended to injured conspecifics more so than to non-injured conspecifics; moreover, thermal imaging revealed that chimpanzees exhibited greater reduction in nasal temperature when viewing an injury rather than a control stimulus. Currently there is no explicit programme for studying emotional targeted helping in animals systematically, in both natural and experimental conditions. In addition, like consolation, forms of helping and cooperative behaviour may lead to personal fitness benefits beyond other-oriented concern, such as reciprocity (Wedekind & Milinski, 2000). However, using these paradigms to compare internal and external responses to the emotions of others across multiple populations within and between species, may help to uncover the affective mechanisms and possible emotional motivations that may underlie *Pan* helping behaviours. A summary of reports of helping, targeted helping, and epimeletic behaviour in bonobos and chimpanzees is provided in Table 5.

IV. FUTURE DIRECTIONS

Some components of empathy have been studied to a greater extent in chimpanzees than in bonobos. Cross-species comparisons indicate greater emotional attentiveness and perspective-taking abilities in bonobos than in chimpanzees, but systematic comparisons across these components are generally lacking. Here, we describe examples of where future research may focus, to uncover whether species differences are pronounced in these behaviours, as well as additional approaches that could reveal deeper insight into *Pan* emotional understanding.

(1) Socio-cultural aspects of empathy

Great ape societies have been shown to vary socio-culturally, whereby social and even arbitrary behaviours emerge and are culturally transmitted, such as grooming traditions (van Leeuwen *et al.*, 2017*b*) and the 'grass-in-ear' behaviour observed by van Leeuwen, Cronin & Haun (2014). If consolation involves a learned component, it could well follow similar group-specific functions and individual responses may vary across social cultures. As consolation has been observed in most *Pan* communities tested (Fuentes *et al.*, 2002), yet differs in rarity (Arnold & Whiten, 2001; Kutsukake & Castles, 2004), its expression may be dependent on variable social dynamics. Empathy expressions have been shown to vary across human cultures (Chopik, O'Brien & Konrath, 2017). It is likely that proclivity of behaviours such as consolation and emotional contagion may vary across the diverse societies of our closest living relatives too, being contingent on social composition and group structure. Cultural differences may also be reflected in the trends observed between different groups, such as inconsistencies in sex effects. The dominance structure in the captive group studied by Romero *et al.* (2010) may facilitate a more tolerant environment for females and they may play a more involved role in conflict management than in other groups. To understand these species at more length, it may be appropriate to focus less on how they differ between species but how collective temperaments and inter-individual dynamics vary between groups.

The Social Constraints Hypothesis (de Waal & Aureli, 1996) posits that consolation depends on the social tolerance levels of a given social structure. In social primates, the risks of further aggression for potential bystanders appear to be lower in more tolerant societies (Fraser *et al.*, 2009), and this may have facilitated the emergence of consolation in the most tolerant species. Palagi *et al.* (2014*a*) compared two macaque species differing in social tolerance in their social structures. They found that consolation was present in the tolerant Tonkean macaques and absent in the despotic Japanese macaques. Consolation was biased towards close grooming partners and predicted a reduction in victim self-scratching, therefore following the trends seen in *Pan*.

Whilst bonobos were traditionally considered generally more socially tolerant than chimpanzees (Scott & Baillargeon, 2017), collective temperaments and social tolerance have been shown to vary across sanctuary-living *Pan* groups (van Leeuwen *et al.*, 2023), even indicating greater differences within species than between them. As tolerance has been linked with prosocial and empathic responses

Table 5. Compilation of literature investigating various forms of helping and epimeletic behaviour in bonobos and/or chimpanzees, including key relevant findings. Abbreviations: C = captive; S = sanctuary; W = wild; [a] = anecdotal; [e] = experimental; *pp* = *Pan paniscus*; *pt* = *Pan troglodytes*.

Species	Reference	N	Setting	Evidence of helping	Details
P. paniscus	de Waal (2019)	Anecdotal	C	Epimeletic behaviour[a]: Supported	Bonobos alerted zookeepers to individuals trapped in dry moat
P. paniscus	Tan & Hare (2013)	14	S	Altruistic helping[e]: Supported	Will forgo food for the benefit of interacting with strangers
P. paniscus	Tan *et al.* (2015)	7	S	Helping[e]: No support	No other-regarding preferences
P. paniscus	Tan *et al.* (2017)	16	S	Helping[e]: Supported	Positive other-regarding preferences to unfamiliar conspecifics
P. paniscus	Tokuyama *et al.* (2012)	Anecdotal	W	Targeted helping[a]: Supported	Helped trapped groupmate remove snares
P. paniscus; *P. troglodytes*	Amici *et al.* (2014a)	*pp* = 9, *pt* = 12	C	Helping[e]: No support	Negative other-regarding preferences
P. troglodytes	Amati *et al.* (2008)	Anecdotal	W	Targeted helping[a]: Supported	Helped trapped groupmate remove snares
P. troglodytes	Boesch (1991)	Anecdotal	W	Targeted helping[a]: Supported	Affiliating with and helping injured group members
P. troglodytes	Claidière *et al.* (2015)	16	C	Prosociality[e]: Supported	Contagious prosociality
P. troglodytes	Crockford *et al.* (2012)	33	W	Perspective-taking[e]: Supported	Informing ignorant group members of specific threats rather than knowledgeable individuals
P. troglodytes	Goodall (1986)	Anecdotal	W	Targeted helping[a]: Supported	Chimpanzees help injured group members
P. troglodytes	Greenberg *et al.* (2010)	12	C	Helping[e]: Supported	Positive other-regarding preferences
P. troglodytes	Hepach *et al.* (2019)	25	C	Helping[e]: Supported	Chimpanzees provided others with what they wanted, even if it would not help them
P. troglodytes	Hirata (2009)	Anecdotal	C	Targeted helping[a]: Supported	Chimpanzee mothers rescuing infants from dangerous situations by watching and acting accordingly
P. troglodytes	Horner *et al.* (2011)	7	C	Helping[e]: Supported	Positive other-regarding preferences
P. troglodytes	Jensen *et al.* (2006)	5	C	Helping[e]: No support	Negative other-regarding preferences
P. troglodytes	Melis *et al.* (2011)	14	S	Targeted helping[e]: Supported	Positive other-regarding preferences
P. troglodytes	Mendonça *et al.* (2018)	6	C	Helping[e]: Supported Altruistic helping[e]: No support	5/6 preferred prosocial over selfish or altruistic options; preferred selfish when choosing between selfish and altruism
P. troglodytes	Nishida & Hiraiwa-Hasegawa (1985)	Anecdotal	W	Targeted helping[a]: Supported	Chimpanzees help injured group members
P. troglodytes	Pruetz (2011)	Anecdotal	W	Targeted helping[a]: Supported	Young male assisted unrelated female by carrying infant when female could not
P. troglodytes	Silk *et al.* (2005)	7 + 11 pairs	C	Helping[e]: No support	Negative other-regarding preferences
P. troglodytes	Vonk *et al.* (2008)	7	C	Helping[e]: No support	Negative other-regarding preferences
P. troglodytes	Warneken & Tomasello (2006)	3	C	Altruistic helping[e]: Supported	Positive other-regarding preferences
P. troglodytes	Warneken *et al.* (2007)	36	S	Altruistic helping[e]: Supported	Helped unfamiliar individuals
P. troglodytes	Yamamoto *et al.* (2009)	9	C	Targeted helping[e]: Some support	Positive other-regarding preferences
P. troglodytes	Yamamoto *et al.* (2012)	5	C	Targeted helping[e]: Some support	Positive other-regarding preferences

(de Waal, 2008), one might expect that more tolerant groups of chimpanzees or bonobos would show more consolatory tendencies than less-tolerant groups.

Empathic responsiveness may fluctuate if social developments culminate in a higher personal and or interpersonal benefit through engaging in more consolatory responses. For example, in the case of consolation, the proclivity for redirected or renewed aggression may differ depending on collective temperaments and the individual personalities of the involved parties. However, research demonstrates that consolatory tendencies are temporally stable across chimpanzee lifespans (Webb *et al.*, 2017), indicating that empathic behaviour may reflect individual personality characteristics and is not as vulnerable to group/cultural changes. Longitudinal studies across multiple groups in parallel with objective measures of collective temperaments are needed. Such data can be compared with records of affective responses through the non-invasive methods highlighted previously, so as to assess the longevity and association of individual responsiveness and what factors may influence it over time.

(2) Reassurance

A consistently observed behaviour across *Pan* and human cultures is the use of reassurance behaviour – affiliative body contact used to reduce anxiety or aggressive tendencies in another individual (van Hooff, 1967; de Waal, 1989) – during socially tense situations. Aggression can be common for large groups of primates living in environments that foster competition. To alleviate such tension during high-anxiety periods and prevent conflicts, individuals may offer and seek social reassurance, often from more dominant group members (Goodall, 1986; de Waal, 1986, 1992). Reassurance can occur through gestural and physical body contacts and has been observed in wild chimpanzees responding to the vocalisations of unfamiliar conspecifics (Herbinger *et al.*, 2009). Despite being regularly referenced in the literature, little is known about whether affective mechanisms underlie these behaviours nor how they may relate to consolation, which itself represents a context-specific form of reassurance.

As discussed, pre-emptive protection has been considered a measure of empathic targeted helping. Whilst conflict resolution has been documented extensively in the human and animal literature, pre-emptive prevention of conflicts – which may involve protecting the self as well as kin or other group members – through emotional recognition and action has rarely been discussed. Yet, through studying reassurance, we may be able to tap into a different level of emotional awareness and uncover the strategies that chimpanzees and bonobos use to alleviate social tension, prevent conflicts from occurring, and thus maintain group cohesion and stability.

An extensive repertoire of reassurance behaviours for both species has been identified, with significant overlap, including mount and embrace, genital inspection, and begging (de Waal, 1988; Goodall, 1989). Bonobos tend to engage in greater sexual reassurance, including ventro-ventral genital rubbing (de Waal, 1988). Post-conflict affiliation, including consolation, is a context-specific form of reassurance between victims of conflicts and uninvolved bystanders (Romero *et al.*, 2010; Clay & de Waal, 2013). In these situations, they appear to be deployed to reduce conspecific distress, which in turn may prevent redirected aggression towards other group members or future instances of aggression towards the consoler. In non-conflict high-tension contexts, these behaviours may be used to alleviate anxiety in the initiator and receiver alike, during a period of high risk of aggressive interactions.

Reassurance offers the opportunity to look at a potential means of pre-emptive protection of the self, kin, and other group members, through understanding the anxiety felt in conspecifics and taking prosocial actions to help reduce that anxiety. As has been highlighted, empathic behaviour need not be entirely altruistic, so reassurance contacts may be motivated simply by self-protection. Nevertheless, individuals may need to comprehend conspecific anxiety and assess the relative risk of aggression faced. Therefore, it would be reasonable to predict that reassurance contacts may increase with individual- and/or group-level tension, measurable by observing markers of anxiety, such as self-directed behaviours and particular vocalisations and gestures. Furthermore, the differences in resource value and distribution may also influence the propensity to engage in these behaviours. Individuals may also be more likely to direct their attention towards those most likely to be aggressive but would also be expected to seek reassurance from kin and close social contacts (Preston & de Waal, 2002).

Reassurance behaviour among primates, including chimpanzees and bonobos, is especially common during periods of high anxiety such as pre-feeding (de Waal, Aureli & Judge, 2000; Paoli *et al.*, 2007). Studying reassurance would be most appropriate in these settings as they typically offer disciplined feeding schedules that would provide enough pre-feeding time for observations (Young, Khalil & Wharton, 2018). Great ape sanctuaries are particularly suited to this type of research with varying group sizes and fluctuating food competition, thereby likely influencing the form, function, and frequency of reassurance behaviours. Systematic comparisons can be made between groups as well as settings and species, as seen in social tolerance comparative research in bonobos and chimpanzees (van Leeuwen *et al.*, 2023).

(3) Play

Whilst empathic reactions to negative states, such as anxiety and distress, have been observed comprehensively in bonobos and chimpanzees, comparatively less research has emphasised empathic responses to positive emotional expressions. Whilst also used as a means to reduce social tension in competitive contexts, such as prior to feeding (Palagi, Cordoni & Tarli, 2004*a*; Norscia & Palagi, 2011*a*), play behaviour is also considered a means for primates to create and develop social relationships (Palagi, 2018), and thus may also facilitate the sharing of positive emotional states.

Assisted by mimicry and interactional synchrony, positive expressions of emotion are used to promote cooperation and social communication in humans and other primates, increasing affiliation, empathic tendencies, and general pro-social behaviour (Yu *et al.*, 2018). Positive emotional expressions, such as laughter, have been detected as contagious in humans (Provine, 1992; Coviello *et al.*, 2014). Mimicry has been observed in myriad species, regardless of sociality and cognitive capacity, in negative, positive, and ambiguous contexts (Kret & Akyüz, 2022). Thus, it would be insightful to see if empathic reactions to negative emotions correlates with empathic reactions to positive emotions.

Social play in *Pan*, particularly play fighting, appears fundamental for infant development, representing a 'springboard' into the social world (Palagi, 2018). Furthermore, play appears to have a positive effect in reducing social tension among adult male chimpanzees (Yamanashi *et al.*, 2018) and is observed along with sexual behaviour during crowded feeding-anticipation scenarios in bonobos (Paoli *et al.*, 2007). It is well documented that primates communicate their motivations during play through the play-face and facial mimicry (Davila-Ross, Menzler & Zimmermann, 2008; Mancini, Ferrari & Palagi, 2013; Scopa & Palagi, 2016; Palagi *et al.*, 2019), as well as laughter (Davila-Ross, Owren & Zimmermann, 2009). Tacconi & Palagi (2009) found contact play sessions were much less likely among bonobo dyads more prone to agonism, and that play signals increased in a less-safe environment, indicating a higher need for reassurance of motivation when aggression may be more likely. The use of facial mimicry and laughter as communicative signals may serve to lengthen play bouts and reduce the possibility of the interaction descending into a conflict through motivation misinterpretation.

It should be noted that, as with other previously mentioned empathy and social behaviours, the presence and proclivity of play may be mediated by levels of social tolerance within the group. A comparison of two macaque species found that the tolerant Tonkean macaques engaged in more play overall and more adult play than the despotic Japanese macaques (Ciani *et al.*, 2012). Whilst adult chimpanzees do play, often in a competitive way (Cordoni *et al.*, 2023), adult bonobos have been suggested to engage in play more often than adult chimpanzees (Palagi, 2006; Palagi & Cordoni, 2012). There remains a lack of comparative studies on this issue. This potential species difference is posited to be due to an ontogenetic delay in social inhibition (Wobber, Wrangham & Hare, 2010), but may also be representative of varying social tolerance levels of the studied groups.

Future studies are needed to explore whether bystanders may have similar other-oriented responses in this context compared with post-conflict contexts. Moreover, such studies could test whether there is an association between emotional sensitivity to negative expressions and positive expressions. While such questions are understudied, a limitation of such a proposed direction is that findings would be biased towards younger individuals, as infants and juveniles are more likely to engage in play sessions. This could nevertheless yield significant insights into the development of socio-emotional competence. However, *Pan* adult play can be common among certain colonies (Palagi & Paoli, 2007; Palagi, 2008) and is a notably understudied research topic.

V. DISCUSSION

As with humans, strong social support networks are important for our closest living primate relatives. The empathy-related behaviours outlined herein facilitate the growth of such relationships. These behaviours have consistently been observed in both *Pan* species, including mimicry, consolation, and targeted helping (Gruber & Clay, 2016). However, direct comparisons so far only indicate that bonobos have greater perspective-taking abilities. Observational and experimental reports suggest that, across other empathy paradigms, neither species excels over the other. The lack of clarity is primarily due to a lack of direct species comparisons. Some of these behaviours, such as the case reports of epimeletic helping, are impossible to study systematically as they rely on opportunistic observations. However, wild *Pan* individuals have been observed to offer support to fellow group members following or during distressing and difficult circumstances.

Bonobos appear to have greater social attentiveness to conspecifics than chimpanzees (Kano *et al.*, 2015), and show rapid responses towards others' emotional expressions (Kret *et al.*, 2016). These tendencies may be facilitated by different biological mechanisms, whereby chimpanzees, but not bonobos, appear to have deletion of the DupB region in the *AVPR1A* gene, which facilitates a microsatellite called RS3 (Staes *et al.*, 2014). RS3 is associated with social bonding, and increased levels in bonobos may support their reported xenophilia. This is further supported by neurological research, which shows that bonobos have twice the density of serotonergic axons in the amygdala (Stimpson *et al.*, 2016). In addition, Rilling *et al.* (2012) found that, compared to chimpanzees, bonobos have more grey matter in the right dorsal amygdala and right anterior insula, regions associated with perceiving distress in oneself and others. Further, the pathway linking the amygdala with the ventral anterior cingulate cortex is also larger in bonobos. This pathway is implicated in the control of reactive and proactive aggressive impulses. Therefore, these differences support increased emotional sensitivity and inhibition in bonobos but may also explain why more severe conflicts and escalation of conflicts tend to occur in chimpanzees.

These neuroanatomical differences may reflect interspecies differences in emotional regulation and social cognition, including empathy-related behaviours. However, other characteristics that appear to facilitate empathy do not vary between species as much as previously thought. Bonobos have previously been declared to be the more socially tolerant species (Hare *et al.*, 2007), a factor that appears to be crucial for facilitating behavioural manifestations of

empathy. A recent co-feeding within-group experimental study tested captive and semi-wild populations of bonobos and chimpanzees and found social tolerance levels in fact appeared to vary more within species than between them (van Leeuwen *et al.*, 2023). It should be noted that this tolerance overlap extends only to within-group conspecifics. Whilst chimpanzees are exclusively hostile to outgroups and many bonobo intergroup encounters result in agonism and threat vocalisations (Clay, Furuichi & de Waal, 2016; Furuichi, 2020), some bonobo societies have been seen to have more tolerant intergroup encounters, typically when feeding competition is lower (Sakamaki *et al.*, 2018; Lucchesi *et al.*, 2020*b*).

Furthermore, the opportunity to provide empathy-related responses, such as consolation and helping behaviour, may be disproportionately larger in chimpanzees than bonobos, due to the difference in social dynamics. The need to console and reduce social tension is possibly much higher in chimpanzees due to the structure of their hierarchies and a much higher risk of aggression and injury (Hare *et al.*, 2012; Wilson *et al.*, 2014). The politics of a chimpanzee society may lend itself to increased rates of empathic behaviour, as individuals seek to maintain group cohesion and protect their personal status and kin.

Bonobos and chimpanzees are two of the most studied primate species regarding empathy and other emotional capacities. It has been suggested that bonobos may be more empathic than chimpanzees due to generally exhibiting less-severe aggression (Parish, de Waal & Haig, 2000; Hare *et al.*, 2012), and what seems to be a neurological predisposition for stronger social and emotional attentiveness (Kano *et al.*, 2015; Kret *et al.*, 2016). Yet thus far there is no direct comparative evidence to support such a statement. Whilst many primates have been observed responding in more basal empathy-related paradigms, such as mimicry and contagion, the *Pan* species have consistently been observed to use multiple forms of empathy. Some of these responses, including consolation, emerge early developmentally and appear to remain consistent ontogenetically (Webb *et al.*, 2017). The early development of sensitivity to the emotions of others may facilitate the emergence of different empathic responses and emotional understanding at younger ages.

A combination of new and established empathy research methods offers a broader and more nuanced approach to understanding the functions of empathy. Whilst bonobos excel (relative to chimpanzees) in perspective-taking and emotional sensitivity, the species appear to overlap in how they respond to the states of others. Both bonobos and chimpanzees appear to perceive the states of others in sophisticated ways. Furthermore, whilst bonobos may have better perspective-taking abilities, both species appear capable of comprehending and processing other's beliefs. Finally, when fellow group members are in distress or need specific assistance or support, both species are capable of providing consolation and targeted help. However, chimpanzees may be less likely to offer targeted help spontaneously to others, a possible species difference that requires direct systematic comparison.

Studying our closest living relatives provides insights into the origins of our own social and emotional behaviour. As we share a close evolutionary history with bonobos and chimpanzees, studying their expressions of empathy may elucidate the journey of how modern human empathy developed through our ancestral lineage. However, we share more than this close genetic history with *Pan*. We overlap with many aspects in our social structures and capacity for physical and social cultures. We also appear to share empathy-related behaviours, ranging from mimicry and contagion, to comforting of distressed conspecifics and epimeletic helping.

Still, there seems to be a divide between human and ape empathy. Some socio-cognitive behaviours, such as false-belief understanding based on explicit behavioural choices, are yet to be identified in *Pan*. Similarly, true helping in experimental tasks has been difficult to determine, due to task design and use of biased samples, consisting of apes raised in restricted, man-made environments. Importantly, though, certain behaviours once thought to be facilitated by language have been shown to be present in pre-verbal infants and non-human apes (Scott & Baillargeon, 2017). The continued use of non-traditional techniques for tasks such as perspective-taking, may continue to reveal that these capacities can emerge in the absence of human language through underlying shared mechanisms.

With the progression of animal empathy research has come the understanding that animals possess the building blocks of morality, as concepts such as reciprocity, conflict resolution, and cooperation are incorporated into animal societies (de Waal, 2008). Yet, despite the growth of research into ape social cognition, a systematic programme that truly incorporates all we know about great ape empathy is lacking. More cross-species investigations would be insightful for making comparisons across phylogeny. The multidimensional view of empathy as a process, varying in levels and combinations of complexity, from emotional contagion to theory of mind, enables us to study behaviours in other species, and thereby evaluate the origins of human social and moral nature.

VI. CONCLUSIONS

(1) Humans and our closest living relatives, bonobos and chimpanzees, rely on strong social support networks for their well-being. Empathy-related behaviours, including emotional contagion, consolation, and targeted helping, play a significant role in building and maintaining these relationships.

(2) Bonobos and chimpanzees demonstrate an overlap in how they perceive the emotions of others and respond to their states. While bonobos may excel in perspective-taking, both species show the capacity to comprehend and process others' beliefs. Consolation and targeted helping behaviours are observed in both species when group members are distressed or need specific assistance.

(3) Whilst bonobos and chimpanzees overlap considerably in their expression of empathic behaviours, individuals and

groups vary as a result of ultimate and proximate intraspecific variation. To comprehend fully the intricacies of empathy in our closest living relatives, there is a critical need for more systematic comparative studies to investigate how empathy varies within and between species and contexts.

(4) As our closest living relatives, behavioural investigations of the *Pan* genus offer valuable insights into the evolutionary and ontogenetic trajectory of empathy within our own species. Shared empathy-related behaviours and social structures suggest common underlying mechanisms. Despite some behavioural gaps between humans and apes, the study of empathy in non-human species unveils the building blocks of morality and sheds light on the origins of human social and moral nature.

VII. ACKNOWLEDGEMENTS

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