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Recognition of Visual Kinship Signals in Chimpanzees (*Pan troglodytes*) by Humans (*Homo sapiens*)

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Abstract

Associating with kin provides individual benefits, but requires that these relationships be detectable. In humans, facial phenotype matching might help assess paternity; however, evidence for it is mixed. In chimpanzees, concealing visual cues of paternity may be beneficial due to their promiscuous mating system, and the considerable risk of infanticide by males. On the other hand, detecting kin can also aid chimpanzees in avoiding inbreeding, and in forming alliances that improve kin-mediated fitness. While previous studies assessing

relatedness based on facial resemblance in chimpanzees exist, they employed images of captive populations in whom selection pressures and reproductive opportunities are controlled and only assessed maternity or paternity of adult offspring. In natural populations, the chances of infanticide are highest during early infancy, suggesting that young infants would benefit most from paternity concealment, while adults and subadults would benefit from the detection of all types of kin, including half-siblings. In our experiment, we conducted an online study with human participants, where they had to assess the relatedness of chimpanzees based on facial similarity. To address previous methodological constraints, we used chimpanzee images across all ages, as well as maternal and paternal half-siblings. We found an above-chance detection of kin across all relatedness categories, with stronger detection of father offspring relationships, increased detection with increasing age, and a tendency for detection to be easier in females. Together these findings support the existence of paternity confusion in infant chimpanzees and provide a possible mechanism for incest avoidance and kin-based social alliances in older individuals.

Keywords: kin selection; kin recognition; facial resemblance; chimpanzee

Recognition of Visual Kinship Signals in Chimpanzees (*Pan troglodytes*) by Humans (*Homo sapiens*)

Kin discrimination is the different treatment of kin (individuals who are biological relatives), as opposed to non-kin, primarily by engaging in prosocial behaviour that benefits them. In doing so individuals across taxa enhance their inclusive fitness (Hamilton, 1963, 1964; Belding's ground squirrels (*Spermophilus beldingi*): Sherman, 1981; carrion crows (*Corvus corone corone*): Baglione et al., 2003; grey mouse lemurs (*Microcebus murinus*): Eberle & Kappeler, 2006). Kin discrimination is greatly facilitated by kin recognition, facilitated by behavioural cues such as prior association, and perceptual similarities between phenotypes (Waldman et al., 1988; Tang-Martinez, 2001). Phenotype matching requires a correlation between phenotypic and genotypic similarity involving both signalling of the relatedness in the phenotype and mechanisms that allow for kin recognition via matching yourself to others, or matching of two other related individuals. Matching occurs in diverse species, including humans, and across sensory domains, for example: visual (Parr & de Waal, 1999; Parr et al., 2010; Bressan & Zucchi, 2009; Charpentier et al., 2020), olfactory (Brown & Macdonald, 1985; Mehlis et al., 2008; Krause & Caspers, 2012; Henkel & Setchell, 2018), and audio cues (Rendall et al., 1996; Akçay et al., 2013).

Kin recognition in primates

In species where fertilisation is internal and females mate with multiple males in any ovulatory cycle, including humans, paternity is uncertain. Concealed ovulation and promiscuous mating in many species mean that male primates have no knowledge of or control over conception (Bellis & Baker, 1990). While human societies vary substantially within and between cultures in the occurrence of non-monogamy, it remains widespread (Broude & Green, 1976). In Western societies, rate of nonpaternity is estimated at 1-10% (Anderson, 2006; Wolf et al., 2012) and in others, such as the Himba pastoralists, nonpaternity may be as high as 48% (Scelza et al., 2020). Primate offspring, particularly in humans and other apes, require significant investment by mature carers (regardless of genetic relatedness), especially during the initial vulnerable years of infancy (humans:

Crittenden & Marlowe, 2008; Kramer, 2011; Li et al., 2013; orang-utans (*Pongo sp.*): van Noordwijk et al., 2018; chimpanzees (*Pan troglodytes*): Emery Thompson, 2012; cotton-top tamarins (*Saguinus oedipus oedipus*): Price, 1992). It has been argued that paternal kin recognition mechanisms should be selected for where paternal care is present (e.g., humans: DeBruine et al., 2008), as the biological selection cost of an error is large: either raising an unrelated infant and 'wasting' valuable resources or denying valuable care to an infant to whom they are related. Similarly, in infants, phenotypic signalling mechanisms that promote the likelihood of paternal care (where present) and/or decrease the potential for harm should be selected for. Whether paternal care is present or not, but particularly where it is absent, there may also be a selective benefit to infants' of ambiguity (e.g. ambiguous facial resemblance hypothesis: Brédart & French, 1999; Oda et al., 2002), as the cost of being considered to be unrelated to their father may be considerable, ranging from abuse and neglect to infanticide (paternal care present – humans: Daly & Wilson, 1996; DeBruine et al., 2008; paternal care absent – chimpanzees: Lowe et al., 2019; mountain gorillas (*Gorilla beringei beringei*): Robbins et al., 2013; Hanuman langurs (*Presbytis entellus*): Hrdy, 1974).

Facial phenotype matching provides one option for kin recognition across relationship types and at different stages in life history and has been suggested as a possible mechanism for paternity recognition by fathers based on phenotypic signalling of paternity in offspring (Pagel, 1997). For facial phenotype matching to be present two features are necessary, kinship must be signalled phenotypically in facial features, and there must be a mechanism present that impacts behavioural responses on the basis of these kinship signals. The term 'recognition' may be misleading – an impact on individual fitness does not necessitate that the individual is aware of their relationship, just that their behaviour is modified by their response to phenotypic signals of kinship. Similarly, it may not depend on knowledge of our own facial features. Self-referent phenotype matching (or the 'arm-pit effect'; Dawkins, 1982), has been shown to use visual cues, for example, colour matching by brown-headed cowbirds (*Molothrus ater*; Hauber et al., 2000). And a range of species,

including humans, chimpanzees (Amsterdam, 1972), Asian elephants (*Elephas* maximus; Plotnik et al., 2006), bottlenose dolphins (*Tursiops truncates*; Reiss & Marino, 2001) and Indian house crows (*Corvus splendens;* Buniyaadi et al., 2020), appear capable of recognising their own image in a mirror (Gallup, 1970; Kitchen et al., 1996). But, knowledge of their facial features in wild individuals is likely to be limited (as it might have been for humans prior to the widespread use of mirrors). Kin-recognition also commonly employs matching based on other related individuals by using kin-referent templates (e.g. house mice (*Mus musculus domesticus*): Penn & Potts, 1998; baboons (*Papio cynocephalus*): Alberts, 1999). Thus, behavioural changes in response to facial cues to paternal kinship (father-offspring or paternal siblings) could include kin-referent templates, for example, where the father's offspring resemble the father's known maternal kin (his mother and siblings, the children's paternal grandmother, uncles, and aunts).

Primates including humans, like other social species, benefit from the ability to recognise other individuals within and outside of their social groups, and appear to reliably identify individuals from facial features (review: Pascalis et al., 1999; chimpanzees: Parr et al., 1998; long-tailed macaques (*Macaca fascicularis*): Dasser, 1987; Japanese macaques (*Macaca fuscata*): Tomonaga, 1994; rhesus macaques (*Macaca mulatta*), Parr et al., 1999; Pascalis and Bachevalier, 1998; brown capuchins (*Cebus apella*), Dufour et al., 2006). The ability to recognise kin relationships between individuals from facial features has been shown to be present in some primates (*Mandrillus sphinx*: Charpentier et al., 2020); but evidence for its presence in apes, including humans, remains mixed. Early studies in humans suggested that infants resembled their fathers, but not their mothers (Christenfeld & Hill, 1995), and that this bias was dependent on age and sex – with male children particularly resembling their fathers at around the ages of two to three years (Alvergne et al., 2007). A similar bias for male facial distinctiveness has been suggested across primates (Cellerino et al., 2004; Parr et al., 2010). However, subsequent studies have been unable to reproduce the findings of greater facial resemblance to fathers (Brédart & French, 1999; Oda et al., 2002). The human species picture is particularly complicated by variation in socio-

cultural behaviour. For example, independently of any actual physical resemblance, Western mothers and maternal relatives described babies as resembling their fathers more than their mothers, while independent judges were more likely to accurately detect maternal relationships (McLain et al., 2000).

Kin recognition in chimpanzees

Paternity is never fully certain in apes – extra-group mating has been documented in monogamous species (white-handed gibbons (*Hylobates lar*): Barelli et al., 2013), as well as one-male units (mountain gorillas (*Gorilla beringei beringei*): Nsubuga et al., 2008), but it is especially uncertain in those with a promiscuous mating system, such as bonobos (*Pan paniscus*: Ishizuka et al., 2018) and chimpanzees (*Pan troglodytes*). While female chimpanzees signal sexual availability through large conspicuous genital swelling, these do not provide precise visual signals of ovulation. Maximum tumescence occurs for ~10 days, and while there are slight increases and other cues, such as olfaction, that may refine information on the fertile period within this, these signals do not support the hypothesis that they are reliable indicators (Deschner et al., 2003). When sexually receptive, female chimpanzees typically mate with multiple males, so candidate fathers cannot be sure of paternity (Newton-Fisher, 2014). Social relationships with kin and non-kin are important for chimpanzee fitness (Langergraber et al., 2007; Watts, 2006; Samuni et al., 2018). Male chimpanzees are philopatric and hierarchical, and social support between males is a key strategy for increased position and tenure in the social hierarchy (Nishida, 1983; Sandel et al., 2020; Mitani et al., 2002; Pusey, 1990), which is then associated with greater individual fitness (Newton-Fisher et al., 2010; Boesch et al., 2006; Wroblewski et al., 2009). Female chimpanzees typically emigrate at adolescence, and competition from resident females is a major cost to new immigrants (up to and including infanticide, Townsend et al., 2007; Kahlenberg et al., 2008) who must rapidly develop a new support network. As chimpanzees experience relatively high rates of infanticide, even within stable social groups (Bronikowski et al., 2016; Townsend et al., 2007; Lowe et al., 2018; Lowe et al., 2020; Wilson et al., 2014), there may be substantial cost, for little apparent benefit, in advertising paternity less

ambiguously. Doing so may reduce the risk of infanticide from the father but could increase the risk from multiple other males, who would incur little cost, and benefit from the mother entering oestrous after the infanticide. Thus, the infanticide avoidance hypothesis in chimpanzees would predict ambiguous cues to paternity (Lowe et al., 2020). Indeed, in contrast to humans, there is relatively little evidence for any active paternal investment (Lehmann et al., 2006). There is some evidence that fathers spent more time playing and grooming with their offspring and associate frequently with the lactating mothers of their offspring (Lehmann et al., 2006; Murray et al., 2016; Sandel et al., 2020); however, it is unclear to what extent both opportunities to reproduce with the mother and subsequent association with offspring are mediated by the father's relationship with the mother (rather than more direct paternal investment). For example, male chimpanzees' tendency to provide care to orphan chimpanzees is mediated by the strength of their previous relationship with the mother (Samuni et al., 2019). In contrast, as female chimpanzees appear less likely to initiate within-group infanticide, advertising maternal relationships may incur fewer costs and, in adulthood, both maternal and paternal sibling relationships may offer a mechanism for effective kin-support (Sandel et al., 2020; kin support in adulthood hypothesis).

As chimpanzees have an extended developmental period, with interbirth intervals typically around 5-years (Emery Thompson et al., 2012) and independence from the mother typically only at around 10-years (Goodall, 1986; Nishida et al., 2003), mother-offspring relationships are clear, as are those between adjacent maternal-siblings. Older maternal siblings still frequently associate with their mothers and any younger siblings, if they remain in their natal community (Reddy & Sandel, 2020). However, non-adjacent maternal-siblings, particularly for younger siblings where their older sibling achieved independence relatively early, and paternal-siblings do not spend extended amounts of time together, and so association provides limited cues to relatedness for these individuals.

Chimpanzees are capable of recognizing other individuals by their faces (Parr & de Waal, 1999), and show similar visual face scanning to humans, with a preference for faces over backgrounds and bodies, and a bias towards central facial features – while within these

chimpanzees scan over faces more quickly, focusing more on the mouth, and humans focusing more on the eyes, these were only immediate fixations, and with longer image exposure durations more detailed investigation of faces is possible (Kano & Tomonaga, 2010). While the pressure to detect or conceal specific relationship-types may vary between chimpanzees and humans, chimpanzees may benefit from the ability to signal kinship through phenotype-matching. Captive, trained individuals were able to match images of unfamiliar mother-son pairs (Parr & de Waal, 1999) and all types of parent-offspring images at above chance (Parr et al., 2010). High performance on mother-son and father-daughter pairs in particular suggests visual kin-discrimination may provide a mechanism to avoid inbreeding (incest avoidance hypothesis; Parr et al., 2010). However, as only mature (adult and subadult) chimpanzees were used and only parent-offspring relationships were tested, there were limitations to the hypotheses that could be explored. For example, if visual kin-discrimination functions to impact infant survivorship, as has been argued in humans (Christenfeld & Hill, 1995), it should be detectable in infant faces. Similarly, inbreeding avoidance should also select for kin-detection between mature siblings, in particular paternal siblings who have limited cues available from prior association. Testing these mechanisms in chimpanzee allows us to investigate more directly whether or not chimpanzees can discriminate these cues (e.g. as in Parr & de Waal, 1999). However, to date, there have been no tests of these hypotheses using stimuli from a wild population of apes.

Employing stimuli from wild chimpanzee faces is an important step. Genetic diversity is likely higher in captive populations (indeed artificially so), the mechanisms underpinning both sexual and natural selection are disrupted by both controlled breeding and controlled healthcare so particular phenotypes may proliferate – or be extinguished – in ways that differ from their expression in wild populations. In contrast, using chimpanzee subjects is only possible in captivity, where the small numbers of subjects available and the need for intensive training remains a limitation. An alternative is to use human participants. In addition to chimpanzees being, together with bonobos, our closest genetic relatives, we are also theirs, and humans have been shown to be reliable judges of facial visual markers of

chimpanzee kinship (Vokey et al., 2004; Alvergne et al., 2009b). In the first study, human subjects could correctly identify chimpanzee mother-offspring pairs (Vokey et al., 2004), and in the second human subjects could reliably identify mother-offspring pairs in chimpanzees, gorillas, and mandrills (but not in chacma baboons; Alvergne et al., 2009b). Together these findings suggest that humans are extremely efficient at detecting kinship in primate faces, in particular in those of other great apes, and that species-specific training is not needed to do so. One possible explanation for this is that the substantial similarity in facial features across ape species allows the human mechanism to operate across a broader group of closely related species (Alvergne et al., 2009b) – this poses the interesting question of whether chimpanzees (who appear similarly able to detect kinship through facial features, Parr & de Waal, 1999) would be able to detect human kin relationships. However, is it also possible that humans and other apes' possess species-specific distinct mechanisms for facial kin-recognition. Irrespective of whether humans have different mechanisms for kin recognition to chimpanzees, humans' ability to detect these relationships would provide support for phenotypic signalling of kinship in chimpanzee faces.

The current study

Here we test relationships across five age groups from infant to adult, and four kinship types: fathers and their offspring, mothers and their offspring, paternal half-siblings and maternal half-siblings. We hypothesize that humans will be capable of detecting phenotypic signals of kinship in chimpanzees based on facial resemblance, in accordance with previous findings, but that the strength of the signals available and, as a result, participant success in detecting kinship, will vary with relationship type, and individual sex and age. We predict that while facial signalling of kinship in chimpanzees will be present, it will provide only weak (ambiguous facial resemblance hypothesis; infanticide avoidance hypothesis) signals, shown by greater-than-chance, but not high, success in detecting kin-pairs. We predict that there will be a stronger facial signal of (and so greater success in detecting) parent-offspring relationships (incest avoidance hypothesis). Based on male philopatry and association cues to relatedness available to maternal-kin we predict that there

will be a stronger facial signal of father-offspring and paternal-sibling relationships than mother-offspring or maternal-sibling relationships (incest avoidance hypothesis; kin support in adulthood hypothesis). We predict that facial signals of kinship will increase with age (ambiguous facial resemblance hypothesis; infanticide avoidance hypothesis; incest avoidance hypothesis; kin support in adulthood hypothesis). Current findings on sex effects in chimpanzee behaviour make predicting the impact of sex difficult. Evidence for male facial distinctiveness in several primates, together with male philopatry, the impact of male social relationships on fitness in adulthood (e.g. Langergraber et al., 2007), and the absence of the cues from association available to maternal kin, predict selection for stronger facial signals of kinship in male chimpanzees (male facial distinctiveness hypothesis). In contrast, the apparent bias towards infanticide of male infants (Takahata, 1985; Wilson et al., 2014; Lowe et al. 2020), taken together with the infanticide avoidance hypothesis, predicts weaker signals of kinship in male chimpanzee faces (Table 1).

Table 1

Summary of the predictions of the five hypotheses for facial kin signalling. Note that '-' indicates that no specific predictions are made.

Predictions	Hypotheses				
	Ambigous resemblance	Infanticide avoidance	Incest avoidance	Kin support in adulthood	Male distinctiveness
Facial signalling of kinship	Yes, but weak	Yes, but weak	Yes	Yes	Yes
Parent-offspring easier to detect	-	-	Yes	-	-
Paternal relationships easier to detect	-	-	Yes	Yes	-
Older targets	Yes	Yes	Yes	Yes	-

easier to detect					
Male targets easier to detect	-	No	-	-	Yes

Methods

Materials

We conducted an online citizen-science experiment via the Gorilla.sc web platform, where we asked participants to match images of related chimpanzees based on facial similarity. Stimuli consisted of 180 in-colour photographs of wild East African chimpanzees (*Pan troglodytes schweinfurthii*), living in the Budongo Forest Reserve, Uganda. Images dated from 1995 to 2018. All targets, answers, and most foils were individuals from the Sonso community, who were habituated to human observation during the 1990s (Newton-Fisher, 1997; Reynolds, 2005), and where extensive records of parentage are available. Images of individuals from the neighbouring Waibira community, where habituation began in 2011 (Samuni et al., 2014), were sometimes included as foils.

Age (in years) was included as a predictor in statistical analyses. As we did not have sufficient individuals to match all possible answer options by age in years, we matched target or answer individuals within age categories. Chimpanzees were assigned to one of the following age categories defined by Reynolds (2005): individuals <5yrs classified as infant, 5-9yrs as juvenile, males 10-15yrs as subadult, females 10-14yrs as subadult, and males >15yrs and females >14yrs as adult. We further split the Infant age category into Infant 1: <2yrs and Infant 2: 2-5yrs, as most victims of infanticide are under 2-years old (Kirchoff et al., 2018; Lowe et al., 2020). Age category and maternal relationships were assigned based on long-term demographic data. The identity of fathers was determined by DNA analysis of faecal samples, with a likelihood-based assessment of paternity (see Langergraber et al., 2014).

Following Alvergne et al. (2009b), images were left in colour, close cropped, and presented on a white background, to eliminate any possible bias from backgrounds

(previous research had indicated that this might influence performance in visual kin recognition; Vokey et al., 2004). Images included ears and facial hair, as these represent inherited facial features. Some images had brightness and/or contrast adjusted for better quality. Adjustments were made by HP without any knowledge of the final target-answer pairs, minimizing possible introduction of ambient cues. We processed all photographs using Pixlr Online Editor.

Images in which the chimpanzee subjects faced the camera directly with a neutral facial expression were selected wherever possible; however, as the images were of wild chimpanzees living in a natural rainforest, the quality of the stimuli varied. Some images contained the face at a 45° angle, some had individuals with the mouth open, and some older photographs (necessary to include parent-offspring pairs across ages) were of a lower sharpness or resolution. All photographs were coded for quality on three measures: angle (direct, indirect), mouth (open, closed) and image clarity (clear, blurred). Inter-observer reliability on the coding of these variables was conducted by CH with moderate agreement levels achieved across all variables (Cohen's Kappa: K = 0.67 for blurred images; K=0.83 for angled images; and K=0.63 for images with an open mouth).

Choosing target-answer pairs

Each set consisted of a target image, and four possible response images: one correct answer, and three foils. We included four relatedness-type conditions: mother-offspring pairs, father-offspring pairs, maternal half-siblings, and paternal half-siblings. Each condition had 45 sets, split into three groups of 15 question sets – each question set contained 15 unique target-answer pairs of individuals. We excluded full siblings from the dataset. Human parents and offspring typically have a relatedness (R) of 0.5; and half siblings typically have R of 0.25 where mothers and fathers are unrelated. However, given that chimpanzee communities in the wild are patrilineal, there is relatedness between males in a chimpanzee community (Inoue et al., 2008) and some females stay and reproduce within their natal communities (Walker & Pusey, 2020); thus, the relatedness of pairs in these categories may be slightly higher than is typically seen in a human dataset – as a

result, the wild chimpanzee parent-offspring pairs in our dataset will at least have R of 0.5, and half-sibling pairs at least R of 0.25. All foils were selected to have R of 0.25 or less and be of the same or adjacent age class as the correct response image. Some known relatives with R=0.25 or less (e.g. uncles, grandparents) were used as foils, but only in the mother-offspring and father-offspring sets where the R to be detected was at least 0.5. Foils used in the maternal and paternal half-siblings conditions all had R<0.25. We were unable to match target, answer, and foils on sex in the sibling conditions due to limited stimuli.

For the mother-offspring, and father-offspring sets, the image of the offspring served as the target, while the image of the parent as the answer, following the methodology of previous studies on humans and non-human primates (eg. Alvergne et al., 2009a, b; Oda et al., 2002). For the half-sibling sets, one half-sibling was randomly assigned as the target, while the other half-sibling as the answer. The position of the target among the foils was randomized. While the limited number of individuals, as well as images per individual, made repetition of foil, target, and answer images necessary across the experiment, all possible target-answer pairs in a given condition were included at least once through the three versions of that condition, but not repeated within question sets. While foil images were also repeated within conditions, participants received no feedback on which question set they answered correctly during the experiment, and only a final score out of 15 at the end of the experiment. Therefore, the chance of known ‘wrong’ answers impacting their responses is minimal. Target and possible answer images were matched on facial angle where this deviated from looking straight ahead.

Ethical approval

Participants were provided with full details of the study in advance and asked to complete a consent form before starting the experiment. The experiment was left accessible to younger participants as we feel that the experience was suitable for a child audience and could provide an educational and entertaining tool for children to engage with a STEM topic online. The experiment started with a screen asking participants their year of birth, then redirecting them to one of the three age group appropriate versions of the experiment.

Due to the online nature of the experiment, it was not possible to verify participant age or additional parental consent. Blocking participants under a particular age from accessing an experiment online carries the substantial risk that some participants will not be truthful about their age, in order to access it. We believe that it is more appropriate to design these experiments to be suitable for participants of all ages. All aspects of the study, including providing access to children under 16 years old, were given ethical approval by the Ethical Committee of the School of Psychology and Neuroscience, University of St Andrews (Approval Code PS13177).

Children under the age of 12 completed the questionnaire as an educational game. No data were recorded from them, as we did not feel that it is possible to obtain informed consent for scientific research with this age group online. Older children are capable of giving informed consent when given age-appropriate materials (e.g., Hein et al., 2015). Participants between the ages of 12 and 15 were presented with an age-appropriate information sheet and consent form, were not asked for any demographic information, and received an age-appropriate debrief message at the end of the experiment. Those above 16 were presented with an adult information sheet and consent form, were asked to describe their age group, sex, previous experience with primates, and whether they were re-taking the experiment, then received a debrief message at the end of the experiment. All participants, regardless of age, were free to withdraw from the experiment at any point. The full experimental procedure, including information, consent, and debrief materials for all groups, is published on the Open Materials section of the Gorilla platform under 'Chimp_Faces' https://gorilla.sc/openmaterials/110651

Procedure

Participants were 5315 humans recruited voluntarily online through the Gorilla.sc web platform. The birth year of all participants was collected, and they were directed to an age-appropriate consent form. Participants aged 16 years or older completed an additional demographic questionnaire. The questionnaire asked participants to identify their sex (Female, Male, Other, Prefer not to disclose), age group (16-20, 21-30, 31-40, 41-50, 51-60,

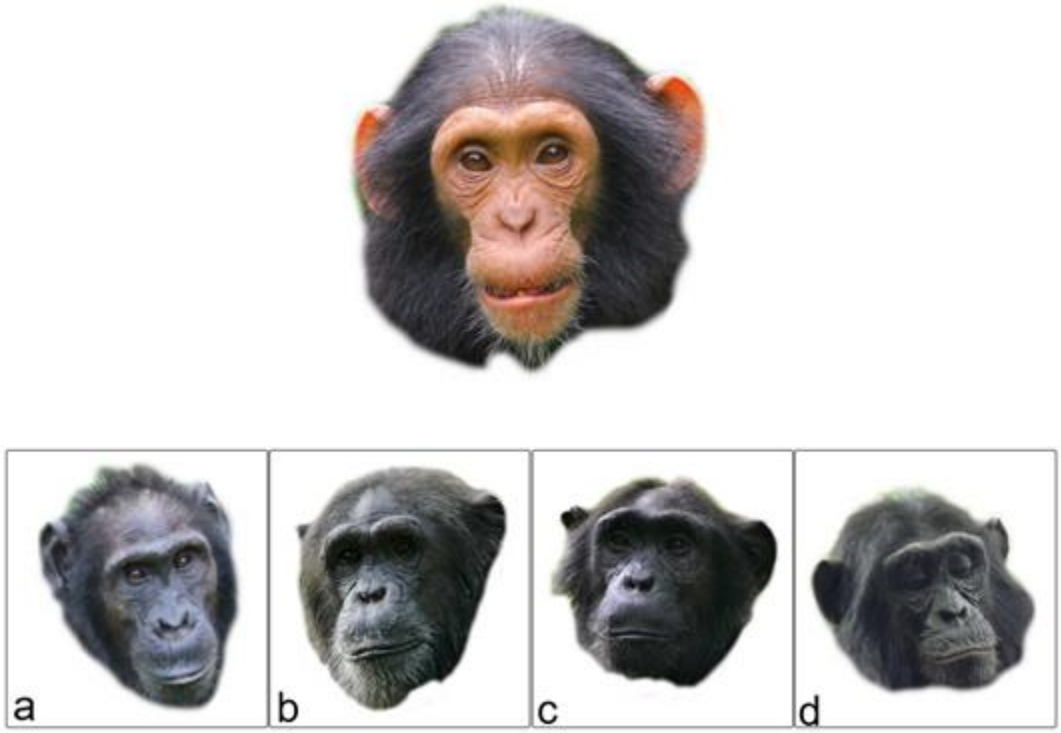
60+), whether they had previous experience with primates (No, Yes (0-2 years), Yes (3-5 years), Yes (5+ years)), and whether they were redoing the test. Demographic data were not collected for participants between the ages of twelve and fifteen. Participants under the age of twelve were allowed to complete the experiment as an educational game, but their responses were not saved.

All participants were randomly assigned to one of the four relationship conditions, and then one of three possible versions of that condition. Due to experimenter error, the participant age group 12-15 were all assigned to the same version of the mother-offspring condition. Each participant received 15 trials, however, participants were free to stop participation at any point, and some (n=2900) did not complete all 15 trials. The order of trials was randomized for each participant.

We followed previous studies in providing short instructions specifying the type of relationship to be detected (e.g., Alvergne et al., 2009a, b; Oda et al., 2002), in this case: whether they had to detect parent-offspring or sibling pairs. Participants were presented with the matching task, where they had to choose the one chimpanzee related to the target chimpanzee out of a choice of four (Figure 1). We instructed them to take as much time as they needed. On each trial, a focus point was shown for 700ms, before the sample image was revealed in the top centre of the computer screen, and the four possible answer images displayed underneath. Participants chose their answer by clicking on their image of choice. After fifteen trials, participants reached the final screen, which included both a debrief and an overall score.

Figure 1

Screenshot of an example trial from the mother-offspring relationship condition



Note: The picture in the top centre is the target, while the four pictures underneath are the possible answer images. Images **a, c,** and **d,** are foils, while the correct answer for the trial is **b.**

Data exclusions

The presence of bots and participants 'clicking through' on online studies is a recognised problem (e.g. Godinho et al., 2019). Answers on which the reaction time was shorter than 2-seconds were excluded, as we judged that to be the minimum time required to look at all presented images and move the mouse to select an option, based on the fastest response time of two authors already familiar with the experimental set-up (HP, CH). Answers with a reaction time larger than three standard deviations from the mean were also excluded as the study was run online and we were unable to control for where participants were distracted from the task for extended periods of time. By excluding responses based on time bounds we risk excluding genuine participants who were particularly fast or slow; however, doing so removed less than 0.01% of our sample, which remained large enough

for rigorous analysis (n=462 excluded by lower bound; n=50 excluded by upper bound, of a total sample n=70423). In contrast, including data that may have been generated by bots or participants clicking through risked introducing error into our dependent variable: human accuracy. One adult participant had missing demographic data – not knowing what caused the error and how it may have influenced their results, we decided to exclude all trials from that participant (n=15).

Data analyses

Statistical analyses were run in RStudio 1.2.5042, running R version 4.0.0 (2020-04-24). Data and code are available in a Github repository (https://github.com/Wild-Minds/ChimpFaces). We analysed n=69895 responses from n=5046 participants. We used a G-test of goodness-of-fit to compare the overall percentage of correct answers to a chance level of one in four (25%).

We fitted two generalised linear models (GLM) using a binomial error distribution and logarithmic link function, following the procedure suggested by Bolker and colleagues (2009) for analysing binomial data. Model 1 – Image Quality characteristics: assessed the impact of target and answer photograph image quality variables on successful judgements of relatedness. Blur, Angle, and Open mouth were included as fixed factors, and answer correctness (Yes/No) as the dependent variable. Model 2 – Participant and Target characteristics: investigated the participant and target characteristics. Participant Age (12-16, 16-20, 21-30, 31-40, 41-50, 51-60, 60+), Participant Sex (Female, Male, Other, Prefer not to disclose), Experience (No, Yes (0-2 years), Yes (3-5 years), Yes (5+ years)), Completion Status (whether the participant had completed all 15 trials, or had left the experiment while it was ongoing: Live, Complete), and Redo (whether the participant indicated that they had previously completed the experiment: Yes, No) as fixed factors, and answer correctness (Yes/No) as the dependent variable.

Factors from Model 1 (Image Quality characteristics) and Model 2 (Participant and Target characteristics) that had an impact on participant correctness were identified on the basis of significance, and were retained as control variables in Model 3 – Chimpanzee

characteristics. These were Blur, Angle, and Open mouth and Completion Status and Participant sex (only the Sex level Male had an effect relative to the reference level, here: Female), so other Sex categories (Female, Other, Prefer not to disclose) were collapsed in Model 3.

To analyse how the proportions of correct responses varied with Condition (Mother-offspring, Father-offspring, Maternal-sibling, Paternal-sibling), Target age (in years), and Target sex (Male, Female) we fitted Model 3 – Chimpanzee characteristics: a logistic Generalised Linear Mixed Model (GLMM; Baayen, 2008) with the function glmer of the R package lme4 version 1.1-23 with the optimizer 'bobyqa' and included these three variables as fixed effects. In addition, the model had Blur (Yes, No), Angle (Yes, No), Open mouth (Yes, No), Completion status (Live, Complete), and Participant Sex (Male; All Other) as fixed control factors, Target identity (N=53), Answer identity (N=56), and Trial number (1-15) were included as random effects. Interactions between fixed effects and random slopes were not included due to incomplete combination matrices. As an overall test of the predictor fixed effects (Condition, Target age, and Target sex) we compared the fit of the full model with that of a null model comprising only the control fixed effects (Blur, Angle, Open mouth, and Completion status) and the random effects of Target identity, Answer identity, and Trial number using a likelihood ratio test (Forstmeier & Schielzeth, 2011; Dobson, 2002; using R function anova with argument 'test' set to "Chisq"). We used the drop1 function to obtain individual p-values for the fixed effects, by systematically dropping each fixed effect from the model one at a time and comparing the reduced model with the full model (Barr et al., 2013). We used the multcomp function to run additional contrasts in order to obtain individual p-values for the separate levels of the fixed effect Condition.

To rule out collinearity we determined Variance Inflation Factors (VIF, Field 2005) for a standard linear model excluding the random effects using the function car, which showed VIF of 1.0 to 1.1 for all fixed effects suggesting no issues of collinearity. We determined the marginal (fixed effects) and conditional (fixed and random effects) effect sizes using the function r.squaredGLMM of the package MuMIn (version 1.43.17). We assessed model

stability by comparing the estimates obtained from the model based on all data with those from the model comprised only the fixed control and random effects excluded one at a time (Nieuwenhuis et al., 2011). This revealed the model to be fairly stable with the exception of the effect of the fixed effect of Angle which overlapped zero. Confidence intervals were derived using the function bootMer of the package lme4, using 1,000 parametric bootstraps and bootstrapping over the fixed control and random effects.

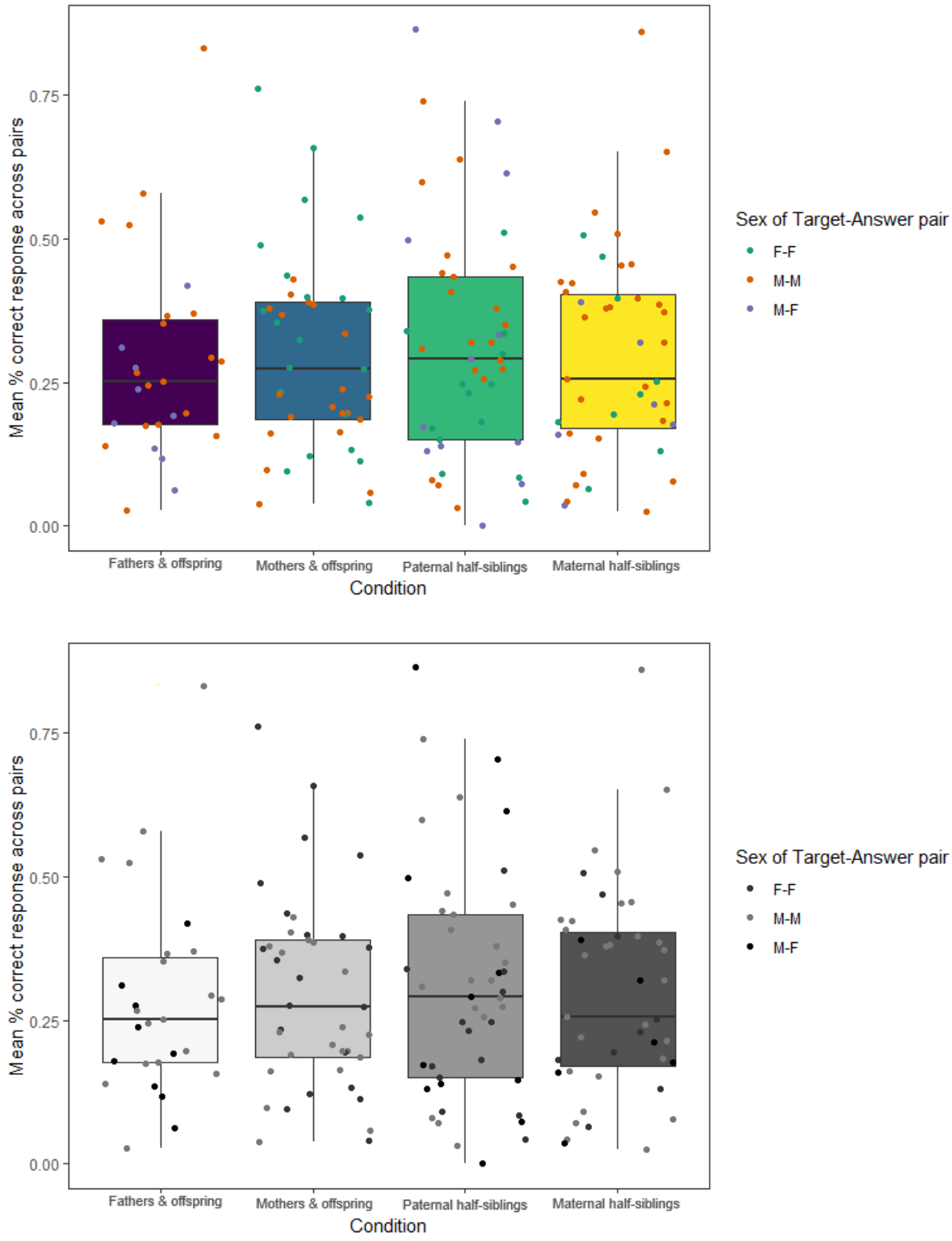
Results

Can human participants identify related chimpanzees based on their facial similarity?

Out of 69,895 answers received, participants correctly identified 20,555, or 29.41% of related chimpanzee pairs. Participants were able to correctly identify related chimpanzees based on their facial features; however, the size of this effect appears small (chance success level=25%; Correct answers mean=29.41% ±45.6%; n=69,895, G-test of goodness-of-fit: $G_{(1)}$=698.72, p<0.001). Mean correct response varied substantially across pairs and included high success >75% for some pairs in all categories of relationship (Fathers and Offspring range: 2.67%-83.25%; Mothers and Offspring range: 3.82%-76.18%; Paternal half-siblings' range: 0%-86.42%; Maternal half-siblings' range: 2.56%-86.01%; Figure 2).

Figure 2

The mean percentage of correct answers across pairs for the four relatedness-type conditions



Note: The four relatedness-type conditions are Fathers and offspring, Maternal-siblings, Mothers and offspring, and Paternal-siblings. One dot stands for the mean percentage of correct answers for one target-answer pair. Colour of the dot represents the sexes of the target-answer pair. The mean percentage of correct answers for each condition is

represented by a solid horizontal line within the respective box, while SE as solid vertical lines at each end of the box.

Do image and participant characteristics influence detection of resemblance?

Out of 69,895 answers, 11,774 included an answer or trial image that was blurred, 10,581 had an answer or trial image that was angled, and 7918 trials had an image with an open mouth. Trials where the target or answer images were blurred were harder to assess (n=11,774 answers, mean percentage correct responses across answers=26.99% ± 44.39) compared to trials with non-blurred images (n=58,121 answers (Table 1). As they affected the assessment of relatedness (Model 1 – Image Quality characteristics, Table 2), Blur, Angle, and Open mouth were retained as control factors in subsequent tests of the impact of relationship-type, age, and sex in Model 3.

Table 2

Parameter estimates for Model 1 – Image Quality characteristics: a binomial GLM for correctness of answer as a function of Blur, Angle, and Open mouth.

Parameter	Correct ~ Blur + Angle + Open			
	Estimate	SE	z value	p
Intercept	-0.84	0.01	(1)	(1)
Blur	-0.14	0.02	-6.05	<0.001***
Angle	0.07	0.02	-2.77	0.006
Open mouth	0.07	0.03	-2.56	0.010

Note: The levels of Blur are Yes, No, the levels of Angle are Yes, No, and the levels of Open mouth are Yes, No. The reference category for all three predictors is No.

(1) Not indicated because of limited interpretive value.

Answers by participants who did not complete the full experiment were correct significantly less often (n=33,289 answers, mean percentage correct responses across answers=28.72% ± 45.25) as compared to participants who completed the full experiment (n=36,606 answers, mean percentage correct responses across answers=30.03% ± 45.84). Similarly, participant sex had a limited impact, with males correct marginally less often (n= 27,099 answers, mean percentage correct responses across answers=28.95% ± 45.35) than females (n=39,730 answers, mean percentage correct responses across answers=29.84% ± 45.76).

No other participant factor affected detection (Model 2 - Participant and Target characteristics, Table 3). Completion status and sex were retained as control factors in subsequent tests of the impact of relationship-type, target age, and target sex in Model 3.

Table 3

Parameter estimates for Model 2 – Participant and Target characteristics: a binomial GLM for correctness of answer as a function of Participant Sex, Participant Age, Redo, Participant Experience, and Completion Status.

Parameter	Correct ~ PSex + Page + Redo + PExperience + Status			
	Estimate	SE	z value	p
Intercept	-0.87	0.09	(1)	(1)
Men	-0.04	0.02	-2.25	0.025*
Other	-0.05	0.09	-0.51	0.613
Unknown	-0.09	0.07	-1.25	0.210
16-20	0.01	0.10	0.15	0.879
21-30	0.09	0.09	0.98	0.326
31-40	0.02	0.09	0.27	0.788
41-50	0.06	0.09	0.64	0.524
51-60	0.02	0.09	0.23	0.816
60+	0.01	0.09	0.17	0.900

Redo	-0.09	0.05	-1.57	0.117
Yes (0-2 years)	0.02	0.04	0.54	0.588
Yes (3-5 years)	0.06	0.08	0.70	0.485
Yes (5+ years)	0.10	0.06	1.66	0.096
Live status	-0.06	0.02	-3.65	<0.001***

Note: The levels of Participant Sex are Women, Men, Other, Unknown, the levels of Participant Age are 12-16, 16-20, 21-30, 31-40, 41-50, 51-60, 60+, the levels of Redo are Yes, No, the levels of Participant Experience are No, Yes (0-2 years), Yes (3-5 years), Yes (5+ years), and the levels of Completion Status are Live, Complete. Baseline Sex is Female, baseline Age is 12-16, baseline Redo is No, baseline Experience is No, and baseline Status is Complete.

(1) Not indicated because of limited interpretive value.

Is resemblance influenced by the relatedness-type, age, and sex of the chimpanzee?

Overall, there was a clear influence of the three main test variables on accuracy of judging chimpanzee relatedness (Model 3 – Chimpanzee characteristics: full-null model comparison in which null model includes all predictors except for Condition, Target age, and Target sex: X^2=410.19, df=5, p<0.0001). The proportion of the variance explained by the fixed effects was $R^2_{marginal}$=0.14, and the proportion explained by the fixed and random effects was $R^2_{conditional}$=0.54.

More specifically, we found that participants were less accurate at matching siblings, in particular paternal siblings, as compared to fathers and offspring. But also, when other factors were controlled for, they were less accurate at judging mothers and offspring, as compared to fathers and offspring (Model 3, Table 4).

In addition, we found that participants were more successful at matching relatedness with increasing age of the target individual, and the sex of the target individual also impacted participant success, with lower success for male targets (Table 4). For the control predictors we found that image Blur decreased success (Blur: -0.22±0.06, z=-4.49, P<0.0001), as did

Face Angle (Angle: -0.16±0.59, z=-2.76, P=0.006), and Participants who dropped out part way through were slightly less successful (Status: -0.07±0.02, z=-3.72, P<0.0001). Participant Sex tended to have a small effect, with men again marginally less successful than other sexes (-0.04±0.02, z=-1.88, P=0.06), as did Open mouth (0.17±0.09, z=1.96, P=0.05).

Table 4

Parameter estimates for Model 3 – Chimpanzee characteristics: a binomial GLMM for correctness of answer as a function of Condition, Target Age, and Target Sex.

Parameter	Correct~Condition+Tage+Tsex					
	estimate	SE	lower CI	upper CI	Z value	p
Intercept	0.73	0.28	0.15	1.34	(1)	(1)
Mothers & offspring	-0.67	0.23	-1.15	-0.15	-2.98	0.003
Paternal siblings	-2.23	0.14	-2.54	-1.91	-15.82	<0.001
Maternal siblings	-1.79	0.13	-2.07	-1.49	-13.52	<0.001
Target Age (2)	0.39	0.04	0.31	0.48	10.72	<0.001
Target Sex (3)	-0.56	0.26	-1.10	-0.04	-2.15	0.031

Note: Baseline value for Condition is Fathers & offspring. The levels of Condition are Fathers & offspring, Mothers & offspring, Paternal siblings, Maternal siblings, Target Age is in continuous years and the levels of Target Sex are Female, Male. We report p-values for the fixed effects Target Age and Target Sex from the drop1 function, and for individual levels within Condition from the multcomp function.

(1) Not indicated because of limited interpretive value.

(2) z-transformed to a mean of 0 and a standard deviation of 1.

(3) Dummy coded with Female as the reference level.

As initial analysis of the full data set showed high-standard deviation in some results, we ran a duplicate analysis using the full sample prior to data exclusions (which removed less than 0.001% of the sample) in order to assess the robustness of our findings. We found no difference in the results between the analysis of the restricted sample, and the full sample with no exclusions. In the full sample with no exclusions out of 70,408 answers received, participant correctly identified 20,688, or 29.38% ±45.6% of related chimpanzee pairs. Again, there was a clear influence of the three main test variables on accuracy of judging chimpanzee relatedness (Model 3b_no exclusions – Chimpanzee characteristics: full-null model comparison in which null model includes all predictors except for Condition, Target age, and Target sex: X^2=375.79, df=5, p<0.0001; for a full summary of the model results see supplemental Table S1).

Discussion

Participants were able to distinguish related chimpanzees based on facial similarities, supporting the claim that information about kinship is encoded in chimpanzee faces, and that humans are capable of cross-species kin facial recognition. Under ideal conditions, where visual challenges like image blur and facial angle were eliminated, accuracy typically remained around 30% (with chance at 25%). However, there was substantial variation across particular pairs of individuals, with some pairs achieving very high detection rates of over 80% accuracy. In general, across individuals and pairs of chimpanzees, detection of facial resemblance in chimpanzees was present but highly variable and typically offered a relatively small, but consistent, improvement above chance in human raters, providing support for the ambiguous facial resemblance hypothesis.

We found no significant effect of participant age, or previous primate experience on accuracy, although a trend indicated that participants with at least 5 years of experience may have been more successful, and we found only a very marginal effect of participant sex; thus, the ability to match related chimpanzees appears widespread. We found that male

chimpanzees' kinship was less easily identifiable than that of female chimpanzees (contra the male facial distinctiveness hypothesis), and a small but clear effect for age: with kinship more easily identifiable as the target age increased (pro the infanticide avoidance, incest avoidance, and kin support in adulthood hypotheses) (Table 5). There were also consistent differences in detection across different types of relatedness, as compared to fathers and their offspring, participants were less likely to detect sibling relationships (in particular, paternal siblings), and less likely to detect mothers and their offspring.

Table 5

Summary of support for the five hypotheses for facial kin signalling.

Predictions	Hypotheses				
	Ambigous resemblance	Infanticide avoidance	Incest avoidance	Kin support in adulthood	Male distinctiveness
Facial signalling of kinship	✓	✓	✓ but weak	✓ but weak	✗
Parent-offspring easier to detect	-	-	?	-	-
Paternal relationships easier to detect	-	-	✓	✓	-
Older targets easier to detect	✓	✓	✓	✓	-
Male targets easier to detect	-	✓	-	-	✗

Note: Dashes indicate that no specific predictions were made, question marks indicate unclear support for predictions, while ticks and crosses indicate the predictions that were supported (✓) or otherwise (✗) by the results.

We find no evidence for a male-bias in facial distinctiveness described in other primate species (rhesus macaques: Parr et al., 2010; humans: Cellerino et al., 2004). While we do appear to find a bias towards detection of fathers and their offspring, as compared to other relationship types, we find that detection of kinship increases with age, which would support the hypothesis that protection from infanticide is served by paternity confusion, rather than advertisement (Hestermann et al., 2001; Newton- Fisher, 2014; Lowe et al., 2019). While we were unable to test it directly, it is unlikely that this age effect was driven by the age difference between the target and their parent in the stimuli, as age differences between half-siblings were smaller and appear harder to detect. Previous studies showing male facial distinctiveness did so by looking at adult individuals. As our data were taken from wild chimpanzees, where females migrate in adolescence, it was not possible for us to fully explore the interaction between sex and age, and it may be the case that male facial distinctiveness is differently expressed across the lifespan.

The lower level of success for half sibling relationships as opposed to parent-offspring relationships may be due to lower levels of relatedness in these individuals ($R \geq 0.5$ for parent-offspring, $R \geq 0.25$ for half-siblings). However, variation in relatedness cannot account for the difference in success of matching father-offspring and mother-offspring pairs. Given chimpanzee philopatry, it is possible that male foils were slightly more closely related to offspring in the father-offspring condition than female foils in the mother-offspring condition; however, if anything this should have made detection of father-offspring relationships more, rather than less, difficult than mother-offspring relationships. Similarly, relatedness between chimpanzee males in the same community could lead to slightly higher relatedness between maternal, as opposed to paternal, half siblings. But, once again our data suggest that between these groups detecting maternal siblings was slightly more challenging. The combination of the detection of father-offspring relationships, and the easier detection of female targets across conditions, are consistent with previous studies of captive populations in which father-daughter relationships were particularly detectable (Parr

et al., 2010), but further investigation of possible interactions between relationship type and individual sex is needed.

Taken together our data supports the ambiguous facial resemblance hypothesis described in humans (Brédart & French, 1999; Oda et al., 2002), in which offspring resemble their fathers, but not too much. In chimpanzees, given limited paternal care (c.f. Lehmann et al., 2006; Murray et al., 2016; Sandel et al., 2020), signalling paternity is likely to serve to increase risk from multiple non-father males, while offering limited - if any - benefits. Accuracy rates across particular pairs of individuals varied, but even within this variation, accuracy in infancy was rarely above 50% for any individual, while in older pairs it could reach over 80%, consistent with predictions by the infanticide avoidance, kin support in adulthood, and incest avoidance hypotheses.

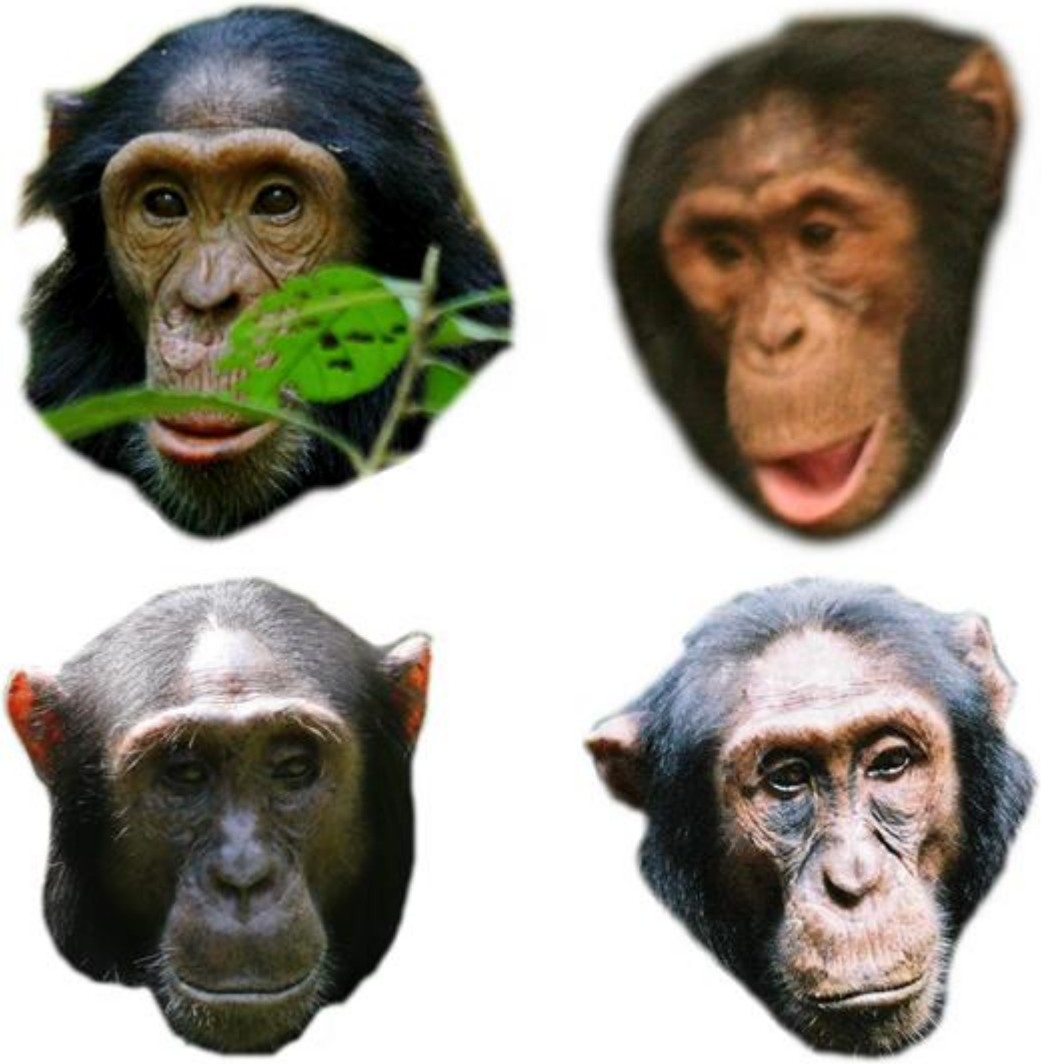
Detection of relatedness across the different types of relationships was, on average, consistently but only slightly above chance, and varied between relatedness-types that shared the same degree of genetic relatedness (for example: fathers and offspring, and mothers and offspring R ~0.5). This variation suggests that facial cues may provide more than just information on generic genetic closeness, and that, as found in mandrills (Charpentier et al., 2020), different types of chimpanzee relatedness may have been under different selection for kin recognition. Relatedness was most easily detected in fathers and their offspring, but least easily detected in paternal sibling pairs. This pattern of results does not clearly fit into any single hypothesis – increased detection of father-offspring relationships provides support for incest avoidance in the absence of cues from association (available in mother-offspring relationships). But the same pattern should then hold for paternal and maternal sibling relationships, whereas here our data suggest the opposite (that paternal sibling relationships may be harder to detect). Chimpanzee females typically emigrate at adolescence (Goodall, 1986; Reynolds, 2005; Walker et al., 2018), however, some individuals remain in their natal communities (Walker & Pusey, 2020), and individuals will typically start reproductive cycles prior to emigration (Nishida et al., 2003; Walker et al., 2018). Both fathers and brothers represent a potential risk of incest, but these relationships

were not similarly detected, suggesting that if visual indicators of relatedness function as an additional cue for incest avoidance (where there is limited information from prior association) this is not similarly selected for across relationship types. However, increasing detection of kinship in older individuals may serve to offset the risk of incest. Another selective advantage of the detection of kin-relationship in both same- and opposite-sex chimpanzee pairs is the formation of coalitions and support in adulthood. Given age differences these may arguably be of more use in sibling relationships, as seen in maternal brothers (Sandel et al., 2020); however, maternal social rank has been shown to co-vary with the rank of their adult sons in bonobos (Furuichi, 1997; Surbeck et al., 2010), and while here the kinship is transparent to both parties, variation in the presence of or benefits from social support between fathers and offspring in bonobos, and either parent and their adult offspring in chimpanzees remains to be investigated.

Interestingly, for particular pairs – across all relationship-types – detection could be very reliable. Large inter-individual variation in facial signalling of kinship suggests limited population wide pressure, instead high-detection in particular pairs may be the result of inter-individual difference in gene expression. For example, unusual facial pigmentation was a feature in some sets of individuals with high detection of kinship (see Figure 3).

Figure 3

Target-answer pair of offspring and their father demonstrating unusual facial pigmentation



Note: The individual on the top left (BG) is an older juvenile female, the individual on the top right (FD) is her adult male father; the individual on the bottom left (KS) is a subadult male, the individual on the bottom right is his adult father (BB); all four show unusually consistent pale facial pigmentation. The images of BG, BB, and KS are clear, closed mouth, and non-angled, the image of FD is blurred, open mouth, and angled.

Future studies could improve on our work in a number of ways – for example, while it is impossible to have wild chimpanzees provide responses to kin relationships in an experimental set-up, the use of large sets of wild stimuli in captive studies where these methods are available could be employed. In addition, within human studies – while it would

substantially restrict sample size – the use of more controlled conditions in direct testing, and, importantly, the use of longer-form within-subjects designs in which each participant rates individuals from across all relationship categories could provide important controls that might narrow the substantial variation we find in our results. In future work it may be of particular interest to explore cues to facial similarity in bonobos (*Pan paniscus*), in whom there are no descriptions of infanticidal behaviour to date, or indeed any conspecific killing, or in West African chimpanzees (*P. t. verus*) in which conspecific killings, including infanticide, appear to be very rare (Furuichi et al., 1998; Fowler & Hohmann, 2010; Wilson et al., 2014). In these species, in the absence of associated risks, cues to kinship may be more freely expressed. Indeed, the strong signals of father-daughter relationships described in previous studies of captive individuals may have been impacted by sub-species effects. While subspecies details were not reported, the Yerkes population of chimpanzees tested are majority *P.t. verus*, or *verus*-hybrid (Ely et al., 2005). It is also likely that chimpanzees incorporate additional cues to assess their relatedness with other individuals, and thus recognise their offspring or kin. For example, chimpanzees also appear able to recognise conspecifics based on their genitals (Kret & Tomonaga, 2016; de Waal & Pokorny, 2008), their vocalisations (Kojima et al., 2003; pant hoots: Mitani et al., 1996), and their smell (Henkel & Setchell, 2018). Exploring the pattern of cues to paternal kinship signalling across *Pan* and *Homo* species and sub-species, would allow us to disentangle the separate possible effects of suppression due to infanticide, or promotion due to paternal care, support in adulthood, or avoidance of incest on the selection of cues to paternal kinship in recent Hominid evolution.

Our results confirm that facial features provide cues to kinship in a wild population of East African chimpanzees. We find no support for male distinctiveness, and our data support the presence of paternity confusion, rather than distinction, in younger chimpanzees. We find evidence that different types of chimpanzee relatedness may have been under different selection for kin recognition, but given the generally weak signal and large inter-individual variation we suggest there has been only limited selection pressure on the expression of

signals for facial phenotype matching in wild chimpanzees.

Author note

We have no known conflict of interest to disclose

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