

Research Article



Psychological Science 1–12 © The Author(s) 2023



Article reuse guidelines: sagepub.com/journals-permissions DOI: 10.1177/09567976221140326 www.psychologicalscience.org/PS



Chimpanzee and Human Risk Preferences Show Key Similarities

Lou M. Haux¹, Jan M. Engelmann², Ruben C. Arslan¹, Ralph Hertwig¹, and Esther Herrmann³

¹Center for Adaptive Rationality, Max Planck Institute for Human Development; ²Department of Psychology, University of California, Berkeley; and ³Centre for Comparative and Evolutionary Psychology, Department of Psychology, University of Portsmouth

Abstract

Risk preference impacts how people make key life decisions related to health, wealth, and well-being. Systematic variations in risk-taking behavior can be the result of differences in fitness expectations, as predicted by life-history theory. Yet the evolutionary roots of human risk-taking behavior remain poorly understood. Here, we studied risk preferences of chimpanzees (86 *Pan troglodytes*; 47 females; age = 2–40 years) using a multimethod approach that combined observer ratings with behavioral choice experiments. We found that chimpanzees' willingness to take risks shared structural similarities with that of humans. First, chimpanzees' risk preference manifested as a traitlike preference that was consistent across domains and measurements. Second, chimpanzees were ambiguity averse. Third, males were more risk prone than females. Fourth, the appetite for risk showed an inverted-U-shaped relation to age and peaked in young adulthood. Our findings suggest that key dimensions of risk preference appear to emerge independently of the influence of human cultural evolution.

Keywords

decision making, chimpanzees, risk preference, risk taking, ambiguity aversion, life span, life-history theory

Received 1/17/22; Revision accepted 10/10/22

Risk preferences contribute to many of the decisions people make—whether to explore new areas in search of food, shelter, or mates; compete for social status; or engage in financial investments, to name but a few (Barseghyan et al., 2013; Brailovskaia et al., 2018; Clark & Lisowski, 2017; Dohmen et al., 2011; Mata et al., 2018; Schonberg et al., 2011; Slovic, 1987). As a key building block in decision processes that shape individuals' health, wealth, and well-being, risk preference has the potential to influence the entire course of an individual's life and therefore presents wide-ranging consequences for society. Yet its biological evolutionary roots remain poorly understood, and tests are scant for the proposition that "modern attitudes to risk are, at least in part, the product of biological evolution" (Robson, 1996, p. 397; see also Karlsson Linnér et al., 2019; Robson, 2001).

Here, we investigated whether risk preferences of chimpanzees (*Pan troglodytes*) are isomorphic to human risk preferences in important respects. Chimpanzees

are an ideal reference (The Chimpanzee Sequencing and Analysis Consortium, 2005): They are one of humans' two closest living relatives; they live in large, mixed-sex social groups; and they have similar developmental stages, with extended infant dependency, a period of adolescence, young adulthood, and long life expectancy of up to 50 years. Chimpanzees occupy a variety of habitats—from savannas to evergreen forests—and face myriad risks in their socioecological environments (de Waal, 1973; Goodall, 1968). There are theoretical reasons to expect evolutionary continuities in risk preferences. According to life-history theory, risk taking differs systematically across stages of life (Stearns, 1992). In the context of reproduction, sexual

Corresponding Author:

Lou M. Haux, Center for Adaptive Rationality, Max Planck Institute for Human Development Email: haux@mpib-berlin.mpg.de

selection and differential parental investment costs (Trivers, 1972) predict lower levels of risk taking in females, who invest more in offspring and are therefore more discriminating in choosing mates. Among young males, reproductive competition for females is thus intense, and young human adult males are predicted and known to take more risks (*young male syndrome*; Wilson & Daly, 1985).

How can one study chimpanzee risk taking and what is known about it? Depending on the definition of risk, in psychology, risk preference (attitude) has often been interpreted to refer to the tendency to exhibit behaviors that, though rewarding, involve some potential harms or losses. In economic theorizing, risk preference refers to the willingness to engage in choices that involve higher variance in outcomes (Mata et al., 2018). Here, we will use both definitions. To behaviorally assess risk-taking behavior, comparative researchers have typically adapted human economic-choice paradigms for use in great apes (Rosati, 2017; Santos & Rosati, 2015). In the commonly used setup, subjects make foraging decisions between a safe option (reliable outcome; e.g., one piece of food) and a risky option (variable option with outcome variance; e.g., 50% chance of getting two pieces of food or nothing). Depending on the methodology and the rewards involved, some studies have found that chimpanzees prove to be-like humansrisk averse, consistently preferring the safe over the risky option (Haux et al., 2021; Keupp et al., 2021); other studies suggest, however, that chimpanzees are risk seeking (Haun et al., 2011; Heilbronner et al., 2008; Rosati & Hare, 2011, 2012, 2013). Furthermore, there is some evidence of an increased sensitivity to social risks (see Calcutt et al., 2019; Haux et al., 2021; Rosati & Hare, 2012). Notwithstanding these mixed findings, many questions about chimpanzees' psychology of risk are unanswered. For instance, does chimpanzees' willingness to take risks correlate across distinct domains (e.g., interactions with venomous animals, intergroup encounters, hierarchy fights) and distinct measures of risk—and, if so, to what extent? Can such a willingness, generalizing across several domains, be regarded as a traitlike preference? Furthermore, previous studies relied on sample sizes ranging from four to 24 subjects and examined relatively narrow age ranges (see De Petrillo & Rosati, 2021). Such sample sizes risk a relatively low statistical power to detect small to medium age and sex effects. Therefore, another open question is whether age- and sex-dependent behavioral effects, perhaps similar to those commonly observed in humans, will emerge.

In addition to the study of risk preferences, revealed in subjects' economic choices, we asked long-time caregivers to rate subjects' willingness to take risks in

Statement of Relevance

Risk preference is central to human activity and has the potential to influence the entire course of our lives. However, the evolutionary roots of human risk preference remain poorly understood. We used a multimethod approach to study chimpanzees (N = 86) from infancy to adulthood to determine whether the willingness to take risks in one of humans' closest living relatives is similar to that in humans. Our results show that chimpanzee and human risk preferences share key structural similarities: Chimpanzees' willingness to take risks manifests as a traitlike preference that is consistent across domains and measures, chimpanzees are ambiguity averse, male chimpanzees are more risk prone than females, and chimpanzees' appetite for risk peaks during young adulthood. These evolutionary continuities are likely to reflect adaptations to similar dynamics in human and nonhuman primate life histories.

domains that represent major classes of risks in chimpanzees' ecology. For instance, caregivers rated behaviors that involve the more psychological definition of risk, that is, behaviors entailing the potential for both rewards and some harms or losses. Consider, for example, the display of competitive behaviors to reach higher ranks in the dominance hierarchy. One question is whether, and to what extent, economic choice behaviors and observed behaviors (rated by caregivers) converge on similar inferences about individuals' risk preferences.

Other studies have investigated what has been or what could be interpreted as aspects of risk-taking behaviors beyond choice in economic paradigms. These studies involve, for instance, research on inhibitory control (e.g., MacLean et al., 2014; delay of gratification: Beran et al., 1999; expectancy: Stevens et al., 2011; patience: Rosati et al., 2007), temperament and personality (e.g., Herrmann et al., 2011, 2015; King & Figueredo, 1997; boldness: Massen et al., 2013; curiosity: Damerius et al., 2017; anxiety: Coleman & Pierre, 2014), cooperation and competition (e.g., Hare et al., 2000; trust: Engelmann et al., 2015; Engelmann & Herrmann, 2016; Haux et al., 2021), and new environments (e.g., unsafe areas: Hockings et al., 2006; responses to novelty: Forss et al., 2015; Kalan et al., 2019; xenophobia: de Waal, 2012; xenophilia: Tan & Hare, 2017). As it is not yet clear how these constructs and measures relate to each other as well as to risk preference as gauged here—for instance, Carter et al. (2012) showed that

current boldness measures may not be interchangeable—we will not further interpret these findings.

Last but not least, our study rests on a cross-sectional design involving animals of different ages from infancy to adulthood. The multimethod approach combines observer ratings (Gosling & Vazire, 2002; McCrae, 1994) with behavioral choice experiments and builds on stated willingness ratings and experimental studies on risk and ambiguity preferences in humans (Dohmen et al., 2011; Ellsberg, 1961). These methodological choices allow us to compare the current results with well-established findings on human risk preferences. We focus on four structural aspects of risk preference. First, to what extent does chimpanzee—like human risk preference (Frey et al., 2017) manifest as a traitlike preference that is consistent across domains in both behavior and observers' assessments? Second, are chimpanzees—like humans (Ellsberg, 1961; Rosati & Hare, 2011; Trautmann & van de Kuilen, 2015)—ambiguity averse, that is, less willing to choose options with unknown risks? Third, are male chimpanzees more inclined to take risks than females, mirroring stable differences in human risk preference (Frey et al., 2021)? Fourth, do age differences in chimpanzees' risk preference mirror those in humans, where risk taking peaks in adolescence and early adulthood and is lower in older age (Frey et al., 2021; Josef et al., 2016; Mata et al., 2016)?

Open Practices Statement

All data are included in this article or in the Supplemental Material available online. All code is available from the authors on reasonable request. The design and analysis plan for this study were not preregistered.

Method

Subjects

Eighty-six chimpanzees (47 females; age = 2–40 years) participated in the study (this sample represents all chimpanzees living in the sanctuaries; see Table S1 in the Supplemental Material for more detailed information about the subjects). Chimpanzees have access to large tracts of outdoor enclosures, including trees, bushes, and climbing structures, and live in large, mixed-sex social groups. All individuals stay in indoor enclosures overnight. Subjects are tested in familiar rooms and are never deprived of food or water for any reason. All testing was strictly voluntary. During testing, a subject could indicate its wish to stop participating at any time by, for instance, heading to the door or not making a choice. Chimpanzees are fed a combination

of fruits, vegetables, and other species-appropriate foods three times daily. The research was noninvasive and carried out in accordance with the guidelines of the Pan African Sanctuary Alliance and the regulations of (a) Ngamba Island Chimpanzee Sanctuary, Wildlife Conservation Trust, in Uganda and (b) Sweetwaters Chimpanzee Sanctuary, Ol Pejeta Conservancy, in Kenya (see the Supplemental Material).

Observer report

Seventeen long-time caregivers rated the perceived willingness to take risks of 86 chimpanzees (47 females; age = 2-40 years; 49 chimpanzees from Ngamba Island and 37 from Sweetwaters). Every caregiver rated all chimpanzees in the respective sanctuary. The mean length of time caregivers knew the chimpanzee was 12 years at Ngamba Island Chimpanzee Sanctuary (SD = 2.38; seven caregivers) and 20 years at Sweetwaters Chimpanzee Sanctuary (SD = 6.39; 10 caregivers). Ratings were given for five relevant domains in chimpanzees' daily lives that expose them to risks, making overt behaviors reveal individual's willingness to take risks: foraging, interacting with snakes, escaping from their territory, competing for higher rank in the dominance hierarchy, and interacting with (human) strangers. Caregivers also gave a domain-general assessment of each chimpanzee's willingness to take risks. Ratings were made on a 5-point scale ranging from 0 (not at all willing to take risks) to 4 (very willing to take risks). We calculated a composite risk score per chimpanzee as the mean of the six risk ratings of all caregivers and determined rank-order stability from caregivers' rankings of the chimpanzees from the least to the most willing to take risks (see the Supplemental Material). Interrater reliabilities were calculated for each individual risk item, as well as for the composite risk score and the risk ranking, using the intraclass correlation coefficient (ICC) formula ICC(2,k). For both sanctuaries, interrater reliabilities were excellent for both the composite risk score (Ngamba Island: .85, 95% credible intervals [CI] = [.77, .90]; Sweetwaters: .9, 95% CI = [.84, .95].94]) and the risk ranking (Ngamba Island: .88, 95% CI = [.82, .93]; Sweetwaters: .94, 95% CI = [.88, .97]).Interrater reliabilities for the individual items are reported in Table S1.

Behavioral experiments

Fifty-five chimpanzees (a subsample of the observer ratings; 31 females; age 6–35 years; 33 chimpanzees from Ngamba Island and 22 from Sweetwaters) passed the familiarization steps (see the Supplemental Material) and subsequently participated in the behavioral experiments.

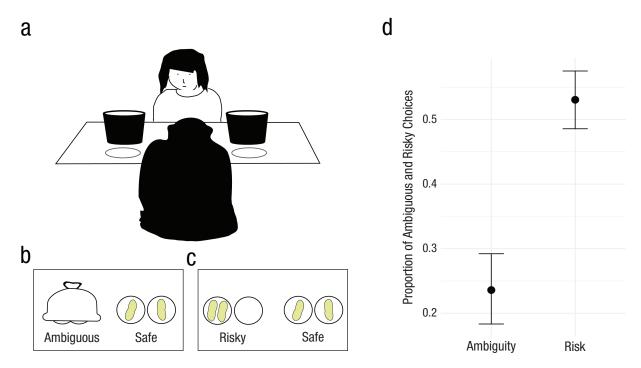


Fig. 1. Ambiguous and risky choices in the behavioral experiments. (a) Experimental setup. (b) Ambiguous condition. (c) Risky condition. (d) Proportion of ambiguous and risky choices. Black dots represent means; error bars represent 95% credible intervals.

Chimpanzees made choices under both risk and ambiguity (Ellsberg, 1961; Rosati & Hare, 2011): In the risky condition, the choice was between a safe and a risky urn (potential outcomes and probabilities were known), and in the ambiguous condition, the choice was between a safe and an ambiguous urn (potential outcomes and probabilities were uncertain). The safe urn always contained one reward; the risky/ambiguous urn contained either two rewards or nothing (50/50 chance; Fig. 1; see also the Supplemental Material).

Results

Correlations across domains and measurements

To examine whether chimpanzees' willingness to take risks manifests as a traitlike preference, we analyzed its consistency across domains and measurement approaches. For the observer ratings, we calculated the correlations among the general and five domain-specific risks (based on grouped means) and the risk rank order. We found high positive correlations between risk domains (Table S2 in the Supplemental Material): They were strongest between general and foraging risk (r = .85, 95% CI = [.77, .90]) and weakest (even though still relatively high) between escape and hierarchy risk (r = .48, 95% CI = [.30, .63]). The risk domains were positively correlated with risk rank order (composite risk

score: r = .53, 95% CI = [.36, .67]). The sole exception was risk in interactions with strangers. It was only weakly correlated with the other risk domains (general risk: r = .10, 95% CI = [-.11, .31]) and negatively correlated with risk rank order (r = -.25, 95% CI = [-.44, -.04]). These divergent findings mirror past results indicating that social risk taking involves an element of trust and thus is rooted in or codetermined by social preferences (Engelmann et al., 2015; Engelmann & Herrmann, 2016; Fehr, 2009; Haux et al., 2021). Next, we investigated the relationship between the observer report and the behavioral risk measure (Table S3 in the Supplemental Material). Importantly, risky choices were positively related to general risk (r = .36, 95% CI = [.06, .60])and risk rank order (r = .38, 95% CI = [.08, .62]). In humans, behavioral and stated risk measures correlate only weakly (M = .06, highest density interval = [.05, .06]; see Frey et al., 2017). In contrast, our behavioral and observational data both indicate that chimpanzees' willingness to take risks manifests consistently across measures.

Ambiguity aversion

To find out whether chimpanzees are ambiguity averse, we investigated the effect of experimental condition (risky vs. ambiguous). The model estimate for the risky condition was positive (b = 1.30, 95% CI = [0.97, 1.65]; Bayesian generalized linear model [BGLM]; Table S4 in

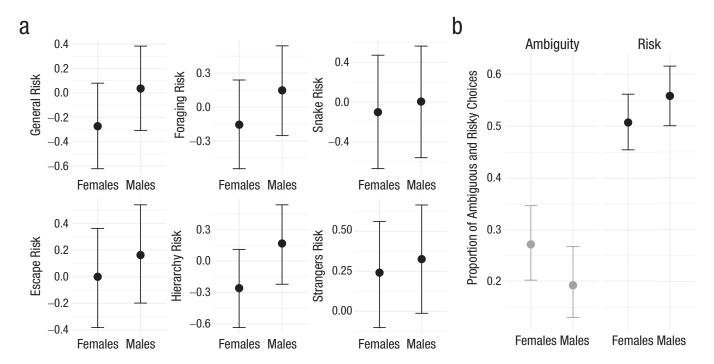


Fig. 2. Sex differences in risk preference. Black dots represent means; error bars represent 95% credible intervals. (a) Sex differences in mean levels of general and domain-specific willingness to take risks. (b) Sex differences in proportion of ambiguous and risky choices.

the Supplemental Material), suggesting that chimpanzees chose the safe urn more often in the ambiguous condition than in the risky condition. As Figure 1d shows, chimpanzees were clearly ambiguity averse (Trautmann & van de Kuilen, 2015), choosing the risky urn in 55% of trials but the ambiguous urn in only 25%.

Sex differences in risk preference

To investigate sex differences, we first analyzed the observer ratings. Male chimpanzees were rated as more risk seeking than females across all domains (Fig. 2a; composite risk score: b = 0.34, 95% CI = [0.04, 0.64], BGLM; Fig. S1a in the Supplemental Material). Consistent with life-history theory, results showed that the sex difference was most pronounced in the hierarchy domain (b = 0.43, 95% CI = [0.13, 0.75]; Table S5 in the Supplemental Material). To compare the size of the sex difference in chimpanzee and human risk preference, we calculated the percentage of the maximum possible (POMP) score for the general risk item of the observer ratings. Chimpanzee males had 8 percentage points of the maximum possible more than females. This corresponds closely to the effect size reported for sex differences in humans (e.g., 6 POMPs; see Dohmen et al., 2011). For the behavioral choices, the model estimate for the interaction of the risky condition and male sex was positive (b = 0.64, 95% CI = [0.01, 1.30]; Model 1.2 in Table S4), suggesting that males were more likely than females to choose the risky urn. Males chose the risky urn in 55% of trials and the ambiguous urn in 20%; females chose the risky urn in 50% of trials and the ambiguous urn in 25% (Fig. 2b). These results again echo those of human studies, showing that males are more risk seeking but also more ambiguity averse than females (Borghans et al., 2009).

Age differences in risk preference

To examine age differences (Fig. 3; see also Table S6 in the Supplemental Material), we used spline-based smooths (Bürkner, 2017). For the composite risk score, the standard deviation (b = 1.29, 95% CI = [0.36, 3.32], BGLM) and visual inspection indicated nonlinearity (Fig. S1b in the Supplemental Material). An inverted-U-shaped relationship emerged consistently across domains and was least pronounced for interaction with strangers (b = 0.76, 95% CI = [0.04, 2.43], BGLM; Fig. 3a and TableS6). This pattern echoes findings in humans showing that the willingness to take risks in the social domain peaks during early adulthood, is lower in older age, and remains relatively stable across the adult life span (Josef et al., 2016). Investigating the interaction of age and sex on the composite risk score revealed an inverted-Ushaped relationship for males (b = 1.62, 95% CI = [0.57, 3.91], BGLM) and a flatter curve for females (b = 0.66, 95% CI = [0.02, 2.61], BGLM; Fig. 4a; see also Fig. S1c and Table S7 in the Supplemental Material). We also

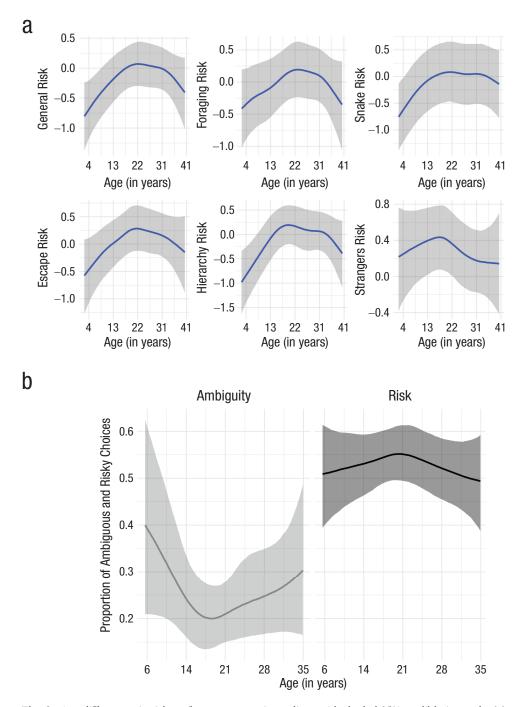


Fig. 3. Age differences in risk preference: regression splines with shaded 95% credible intervals. (a) Age differences (aggregated across male and female subjects) in mean levels of general and domain-specific willingness to take risks. (b) Age differences in proportion of ambiguous and risky choices.

investigated age differences in the behavioral measures (Model 1.3 in Table S4). For choices under risk, a small effect of nonlinearity emerged (b = 0.70, 95% CI = [0.03, 2.31], BGLM). Chimpanzees' willingness to select the risky option was slightly lower in adulthood (Fig. 3b). The peak during young adulthood was less pronounced

for the behavioral risk measure, corresponding to findings in humans showing that stated risk measures pick up age variations that behavioral risk measures do not detect (Frey et al., 2021). As in humans (Josef et al., 2016), male chimpanzees tended to be more risk seeking than females were across all age groups. The willingness

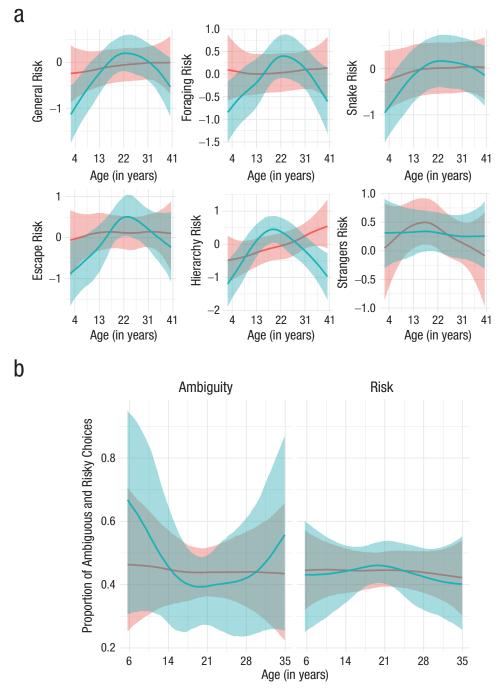


Fig. 4. Age and sex differences in risk preference: regression splines with shaded 95% credible intervals. Red indicates female risk preference, and blue indicates male risk preference. (a) Age and sex differences in mean levels of general and domain-specific willingness to take risks. (b) Age and sex differences in proportion of ambiguous and risky choices.

to select the ambiguous option was highest during child-hood and varied little across adulthood (b = 1.78, 95% CI = [0.24, 4.69], BGLM). Females tended to choose the ambiguous option more often than males did (Fig. 4b).

These results mirror findings in humans showing that ambiguity preferences are invariant over the adult life span and that females are more ambiguity prone than males (Borghans et al., 2009).

Discussion

Risk preference is central to human and nonhuman behavior. The current results demonstrate that chimpanzee and human risk preference share key structural similarities and converge in crucial ways. Consistent with recent findings in humans (Frey et al., 2017), our results showed that chimpanzees' willingness to take risks appears to manifest as a traitlike preference, with high rank-order stability across a set of important domains (based on observers' assessments) and economic choice behavior. The social-risk domain proves to be the exception (Josef et al., 2016). Furthermore, chimpanzees are, like humans, ambiguity averse and less willing to choose options with unknown risks (Ellsberg, 1961; Trautmann & van de Kuilen, 2015). Our results indicate that males are more risk seeking than females, mirroring the same difference in human risk preference (Frey et al., 2021). Finally, chimpanzee risk taking shows an inverted-U-shaped relation to age, peaks in young adulthood, and is lower in older age again mirroring similar trends in humans (Frey et al., 2021; Josef et al., 2016; Mata et al., 2016).

According to life-history theory, risk preference should be elevated in periods in which the goal of reproduction and associated proximal goals (e.g., gaining social status) is paramount (Stearns, 1992). Young adulthood is an indispensable transitional stage for male chimpanzees to learn the techniques of socially mature males in order to establish their own social position (Kawanaka, 1993; Watts, 2018). Consistent with the young male syndrome in humans (Wilson & Daly, 1985), our results show that male chimpanzees are especially risk prone around their 20s and particularly willing to take risks in order to get a better position in the hierarchy. Higher rank is associated with both relatively high mating (Kaburu & Newton-Fisher, 2015; Muller et al., 2011) and paternity (Boesch et al., 2006; Langergraber et al., 2013; Newton-Fisher et al., 2010; Wroblewski et al., 2009) success. Furthermore, our finding of heightened general risk tolerance during young adulthood converges with a recent overview of risk behavior in humans concluding that risk taking is heightened during emerging adulthood (Willoughby et al., 2021).

The current findings, in combination with the multimethod design, enrich the comparative approach in important ways. First, the general and traitlike preference for risk is congruent with evidence suggesting that animal personalities exist across a range of species and that risk-related traits are common characteristics (Wolf et al., 2007). Second, we found that the strangers risk domain was only weakly correlated with the other risk domains. This finding is in line with those of earlier

studies indicating that trusting other individuals is not just a special case of risk taking but is based on important forms of social preferences, such as betrayal aversion (Fehr, 2009; Haux et al., 2021). Moreover, in humans, willingness to trust does not follow an inverted-U-shaped pattern but instead remains relatively stable across the adult life span (Josef et al., 2016). These results fit ideas that in humans and chimpanzees, the social domain remains prioritized across adulthood (Carstensen et al., 1999; Rosati et al., 2020). Third, chimpanzees' observed ambiguity aversion is in line with results by Rosati and Hare (2011). They found that chimpanzees and bonobos are sensitive to ambiguity in the first trials of their experiment, suggesting that subjects dislike choosing options with unknown risks. Yet it remains unclear to what extent chimpanzees knew that only probability but not the information about outcomes was missing. This raises the question of whether ambiguity attitudes in Ellsberg's (1961) implementation of the construct can be measured in nonverbal populations.

Fourth, our results suggest that chimpanzees are risk neutral to (minimally) risk prone. Past research offers inconsistent findings in this regard. The variation in risk sensitivity in studies may be explainable in terms of the presentation and experience of probabilities (see Hau et al., 2010; Heilbronner & Hayden, 2016; Hertwig, 2015; Wulff et al., 2018), that is, whether decisions were based on experienced frequencies (see Calcutt et al., 2019; Haux et al., 2021; Heilbronner et al., 2008; Keupp et al., 2021), or whether subjects had to infer probabilities from the task design (see Haun et al., 2011; Rosati & Hare, 2011, 2012, 2013, 2016). Furthermore, the possibility of coming away empty-handed—whether the risky option included the possibility of receiving nothing or always provided at least some amount of food could also alter the decision (see Haux et al., 2021; Keupp et al., 2021).

Finally, the relatively small sample sizes and the concomitant sex and age distributions of past studies limit the generalizability of previous findings. Future research should expand the multimethod approach, for instance, by including several behavioral measures. This would allow researchers to examine the causes behind the variation in previous work and delineate which task characteristics influence chimpanzee risk sensitivity. Studies involving chimpanzees from different groups and environments will further enrich the discussion about the generalizability of behavioral variations. Because of their early-life experiences, sanctuary chimpanzees might display different risk preferences and behavior from those living in zoos and those in the wild (for a discussion on the generalizability across groups, see King et al., 2005; Laméris et al., 2021; Lutz et al., 2022; Weiss et al., 2007; Wobber & Hare, 2011). Last but not least, because it has been proposed that bonobos (*Pan paniscus*) and chimpanzees (humans' two closest living relatives) show divergent risk preferences (see Rosati, 2017), for a complete reconstruction of our last common ape ancestors preferences, it is essential to also study bonobos' willingness to take risks in more depth in the future.

In the behavioral sciences, risk preference is a mainstay of and a key building block in theories of choice (Barseghyan et al., 2013; Brailovskaia et al., 2018; Clark & Lisowski, 2017; Dohmen et al., 2011; Mata et al., 2018; Schonberg et al., 2011; Slovic, 1987). In recent years, the measurement and stability has been central to the debate about the nature of risk preferences (Frey et al., 2017, 2021; Josef et al., 2016; Schildberg-Hörisch, 2018; Weber et al., 2002). Our multimethod approach can enrich this discussion, indicating that across various aspects of risk preference, both observer ratings (for a discussion on the validity of human ratings, see the Supplemental Material) and behavioral choices are directionally consistent. These findings offer an important first step toward a general mapping of the construct of risk preference in chimpanzees. Understanding the degree of temporal stability and systematic individual change in chimpanzee risk preference will be an important endeavor for future research (Schildberg-Hörisch, 2018). In addition, "actuarial" data such as the frequency of injuries from hierarchy fights will offer another important addition to a multimethod approach to study risk preference in chimpanzees.

In humans, scholars have proposed that the willingness to take risks and to trust others is transmitted across generations through socialization experiences (Dohmen et al., 2012; Roberts et al., 2005; Slovic, 1966) but is also subject to genetic influences (Karlsson Linnér et al., 2019). Our findings suggest that human risk preference may in addition also have deeper phylogenetic roots than previously suspected. Structural similarities in risk preferences of humans and one of our closest living relatives are likely to reflect adaptations to similar dynamics in primate life histories.

Transparency

Action Editor: Lasana Harris Editor: Patricia J. Bauer Author Contributions

Lou M. Haux: Conceptualization; Data curation; Formal analysis; Funding acquisition; Investigation; Methodology; Project administration; Visualization; Writing – original draft; Writing – review & editing.

Jan M. Engelmann: Conceptualization; Methodology; Supervision; Writing – review & editing.

Ruben C. Arslan: Conceptualization; Formal analysis; Methodology; Writing – review & editing.

Ralph Hertwig: Conceptualization; Funding acquisition; Methodology; Resources; Supervision; Writing – review & editing.

Esther Herrmann: Conceptualization; Funding acquisition; Methodology; Resources; Supervision; Writing – review & editing.

Declaration of Conflicting Interests

The author(s) declared that there were no conflicts of interest with respect to the authorship or the publication of this article.

ORCID iDs

Lou M. Haux https://orcid.org/0000-0001-6660-3945 Ruben C. Arslan https://orcid.org/0000-0002-6670-5658 Ralph Hertwig https://orcid.org/0000-0002-9908-9556

Acknowledgments

We thank Lilly Ajarova and Joshua Rukundo, the board members and staff at Ngamba Island Chimpanzee Sanctuary and Wildlife Conservation Trust in Uganda for their crucial support during all stages of this research. We appreciate permission from the Ugandan National Council for Science and Technology and the Uganda Wildlife Authority. We thank Richard Vigne, Samuel Mutisya, Stephen Ngulu, the board members and staff of Sweetwaters Chimpanzee Sanctuary in Kenya for their crucial support during all stages of this research. We appreciate permission from Ol Pejeta Conservancy, Kenya Wildlife Service, and the National Council for Science and Technology. Thanks go to Larissa Samaan and Lukas Eggeling for reliability coding and Susannah Goss for editing. We thank Michael Tomasello, Andrew Whiten and Amanda Seed for feedback. LMH was supported by the German National Academic Foundation and EH by the Minerva Programme of the Max Planck Society. R. Hertwig and E. Herrmann share senior authorship of this article.

Supplemental Material

Additional supporting information can be found at http://journals.sagepub.com/doi/suppl/10.1177/09567976221140326

References

Barseghyan, L., Molinari, F., O'Donoghue, T., & Teitelbaum, J. C. (2013). The nature of risk preferences: Evidence from insurance choices. *American Economic Review*, 103(6), 2499–2529.

Beran, M. J., Savage-Rumbaugh, E. S., Pate, J. L., & Rumbaugh, D. M. (1999). Delay of gratification in chimpanzees (*Pan troglodytes*). *Developmental Psychobiology*, *34*(2), 119–127.

Boesch, C., Kohou, G., Néné, H., & Vigilant, L. (2006). Male competition and paternity in wild chimpanzees of the Taï forest. *American Journal of Physical Anthropology*, 130(1), 103–115.

Borghans, L., Heckman, J. J., Golsteyn, B. H., & Meijers, H. (2009). Gender differences in risk aversion and ambiguity aversion. *Journal of the European Economic Association*, 7(2–3), 649–658.

Brailovskaia, J., Schillack, H., Assion, H.-J., Horn, H., & Margraf, J. (2018). Risk-taking propensity and (un)healthy

behavior in Germany. *Drug and Alcohol Dependence*, 192, 324–328.

- Bürkner, P. C. (2017). Advanced Bayesian multilevel modeling with the R package brms. ArXiv. https://arxiv.org/abs/1705.11123
- Calcutt, S. E., Proctor, D., Berman, S. M., & de Waal, F. B. (2019). Chimpanzees (*Pan troglodytes*) are more averse to social than nonsocial risk. *Psychological Science*, 30(1), 105–115.
- Carstensen, L. L., Isaacowitz, D. M., & Charles, S. T. (1999). Taking time seriously. A theory of socioemotional selectivity. *American Psychologist*, 54, 165–181.
- Carter, A. J., Marshall, H. H., Heinsohn, R., & Cowlishaw, G. (2012). How not to measure boldness: Novel object and antipredator responses are not the same in wild baboons. *Animal Behaviour*, *84*(3), 603–609.
- The Chimpanzee Sequencing and Analysis Consortium. (2005). Initial sequence of the chimpanzee genome and comparison with the human genome. *Nature*, *437*(7055), 69–87.
- Clark, W. A., & Lisowski, W. (2017). Prospect theory and the decision to move or stay. *Proceedings of the National Academy of Sciences*, USA, 114(36), E7432–E7440.
- Coleman, K., & Pierre, P. J. (2014). Assessing anxiety in non-human primates. *ILAR Journal*, 55(2), 333–346.
- Damerius, L. A., Graber, S. M., Willems, E. P., & van Schaik, C. P. (2017). Curiosity boosts orang-utan problem-solving ability. *Animal Behaviour*, *134*, 57–70.
- De Petrillo, F., & Rosati, A. G. (2021). Variation in primate decision-making under uncertainty and the roots of human economic behaviour. *Philosophical Transactions of the Royal Society B*, *376*(1819), Article 20190671. https://doi.org/10.1098/rstb.2019.0671
- de Waal, F. (1973). *Chimpanzee politics: Power and sex among apes*. Johns Hopkins University Press.
- de Waal, F. B. M. (2012). The antiquity of empathy. *Science*, 336(6083), 874–876.
- Dohmen, T., Falk, A., Huffman, D., & Sunde, U. (2012). The intergenerational transmission of risk and trust attitudes. *Review of Economic Studies*, *79*, 645–677.
- Dohmen, T., Falk, A., Huffman, D., Sunde, U., Schupp, J., & Wagner, G. G. (2011). Individual risk attitudes: Measurement, determinants, and behavioral consequences. *Journal of the European Economic Association*, *9*(3), 522–550.
- Ellsberg, D. (1961). Risk, ambiguity, and the Savage axioms. *The Quarterly Journal of Economics*, 75(4), 643–669.
- Engelmann, J. M., & Herrmann, E. (2016). Chimpanzees trust their friends. *Current Biology*, 26(2), 252–256.
- Engelmann, J. M., Herrmann, E., & Tomasello, M. (2015). Chimpanzees trust conspecifics to engage in low-cost reciprocity. *Proceedings of the Royal Society B: Biological Sciences*, 282(1801), Article 20142803. https://doi.org/10.1098/rspb.2014.2803
- Fehr, E. (2009). On the economics and biology of trust. *Journal of the European Economic Association*, 7(2–3), 235–266.
- Forss, S. I. F., Schuppli, C., Haiden, D., Zweifel, N., & van Schaik, C. P. (2015). Contrasting responses to novelty by wild and captive orangutans. *American Journal of Primatology*, 77(10), 1109–1121.

- Frey, R., Pedroni, A., Mata, R., Rieskamp, J., & Hertwig, R. (2017). Risk preference shares the psychometric structure of major psychological traits. *Science Advances*, 3(10), Article e1701381. https://doi.org/10.1126/sciadv.1701381
- Frey, R., Richter, D., Schupp, J., Hertwig, R., & Mata, R. (2021). Identifying robust correlates of risk preference: A systematic approach using specification curve analysis. *Journal of Personality and Social Psychology*, 120(2), 538–557.
- Goodall, J. (1968). The behaviour of free-living chimpanzees in the Gombe Stream Reserve. *Animal Behaviour Monographs*, 1, 161–311.
- Gosling, S. D., & Vazire, S. (2002). Are we barking up the right tree? Evaluating a comparative approach to personality. *Journal of Research in Personality*, *36*(6), 607–614.
- Hare, B., Call, J., Agnetta, B., & Tomasello, M. (2000). Chimpanzees know what conspecifics do and do not see. *Animal Behaviour*, *59*(4), 771–785.
- Hau, R., Pleskac, T. J., & Hertwig, R. (2010). Decisions from experience and statistical probabilities: Why they trigger different choices than a priori probabilities. *Journal of Behavioral Decision Making*, 23(1), 48–68.
- Haun, D. B., Nawroth, C., & Call, J. (2011). Great apes' risk-taking strategies in a decision making task. *PloS One*, 6(12), e28801.
- Haux, L. M., Engelmann, J. M., Herrmann, E., & Hertwig, R. (2021). How chimpanzees decide in the face of social and nonsocial uncertainty. *Animal Behaviour*, 173, 177–189.
- Heilbronner, S. R., & Hayden, B. Y. (2016). The description–experience gap in risky choice in nonhuman primates. *Psychonomic Bulletin & Review*, *23*(2), 593–600.
- Heilbronner, S. R., Rosati, A. G., Stevens, J. R., Hare, B., & Hauser, M. D. (2008). A fruit in the hand or two in the bush? Divergent risk preferences in chimpanzees and bonobos. *Biology Letters*, 4(3), 246–249.
- Herrmann, E., Hare, B., Cissewski, J., & Tomasello, M. (2011). A comparison of temperament in nonhuman apes and human infants. *Developmental Science*, *14*(6), 1393–1405.
- Herrmann, E., Misch, A., Hernandez-Lloreda, V., & Tomasello, M. (2015). Uniquely human self-control begins at school age. *Developmental Science*, *18*(6), 979–993.
- Hertwig, R. (2015). Decisions from experience. In G. Keren & G. Wu (Eds.), *The Wiley Blackwell handbook of judg-ment and decision making* (Vol. 2, pp. 239–267). Wiley-Blackwell.
- Hockings, K. J., Anderson, J. R., & Matsuzawa, T. (2006). Road crossing in chimpanzees: A risky business. *Current Biology*, *16*(17), R668–R670.
- Josef, A. K., Richter, D., Samanez-Larkin, G. R., Wagner, G. G., Hertwig, R., & Mata, R. (2016). Stability and change in risk-taking propensity across the adult life span. *Journal* of Personality and Social Psychology, 111(3), 430–450.
- Kaburu, S. S., & Newton-Fisher, N. E. (2015). Trading or coercion? Variation in male mating strategies between two communities of East African chimpanzees. *Behavioral Ecology and Sociobiology*, 69(6), 1039–1052.
- Kalan, A. K., Hohmann, G., Arandjelovic, M., Boesch, C., McCarthy, M. S., Agbor, A., Angedakin, S., Bailey, E., Balongelwa, C. W., Bessone, M., Bocksberger, G., Coxe, S. J., Deschner, T., Després-Einspenner, M. L., Dieguez, P.,

- Fruth, B., Herbinger, I., Granjon, A. C., Head, J., . . . Kühl, H. S. (2019). Novelty response of wild African apes to camera traps. *Current Biology*, *29*(7), 1211–1217.
- Karlsson Linnér, R., Biroli, P., Kong, E., Meddens, S. F. W., Wedow, R., Fontana, M. A., Lebreton, M., Tino, S. P., Abdellaoui, A., Hammerschlag, A. R., Nivard, M. G., Okbay, A., Rietveld, C. A., Timshel, P. N., Trzaskowski, M., de Vlaming, R., Zünd, C. L., Bao, Y., Buzdugan, L., . . . Beauchamp, J. P. (2019). Genome-wide association analyses of risk tolerance and risky behaviors in over 1 million individuals identify hundreds of loci and shared genetic influences. *Nature Genetics*, 51(2), 245–257.
- Kawanaka, K. (1993). Age differences in spatial positioning of males in a chimpanzee unit-group at the Mahale Mountains National Park, Tanzania. *Primates*, 34(3), 255–270.
- Keupp, S., Grueneisen, S., Ludvig, E. A., Warneken, F., & Melis, A. P. (2021). Reduced risk-seeking in chimpanzees in a zero-outcome game. *Philosophical Transactions of the Royal Society B*, 376(1819), Article 20190673. https://doi.org/10.1098/rstb.2019.0673
- King, J. E., & Figueredo, A. J. (1997). The five-factor model plus dominance in chimpanzee personality. *Journal of Research in Personality*, 31(2), 257–271.
- King, J. E., Weiss, A., & Farmer, K. H. (2005). A chimpanzee (Pan troglodytes) analogue of cross-national generalization of personality structure: Zoological parks and an African sanctuary. Journal of Personality, 73(2), 389–410.
- Laméris, D. W., Staes, N., Salas, M., Matthyssen, S., Verspeek, J., & Stevens, J. M. (2021). The influence of sex, rearing history, and personality on abnormal behaviour in zoo-housed bonobos (*Pan paniscus*). *Applied Animal Behaviour Science*, 234, Article 105178. https://doi.org/ 10.1016/j.applanim.2020.105178
- Langergraber, K. E., Mitani, J. C., Watts, D. P., & Vigilant, L. (2013). Male-female socio-spatial relationships and reproduction in wild chimpanzees. *Behavioral Ecology and Sociobiology*, 67(6), 861–873.
- Lutz, C. K., Coleman, K., Hopper, L. M., Novak, M. A., Perlman, J. E., & Pomerantz, O. (2022). Nonhuman primate abnormal behavior: Etiology, assessment, and treatment. *American Journal of Primatology*, 84(6), e23380. https://doi.org/10.1002/ajp.23380
- MacLean, E. L., Hare, B., Nunn, C. L., Addessi, E., Amici, F., Anderson, R. C., Aureli, F., Baker, J. M., Bania, A. E., Barnard, A. M., Boogert, N. J., Brannon, E. M., Bray, E. E., Bray, J., Brent, L. J. N., Burkart, J. M., Call, J, Cantlon, J. F., Cheke, L. G., . . . Zhao, Y. (2014). The evolution of self-control. *Proceedings of the National Academy of Sciences, USA*, 111(20), E2140–E2148.
- Massen, J. J., Antonides, A., Arnold, A. M. K., Bionda, T., & Koski, S. E. (2013). A behavioral view on chimpanzee personality: Exploration tendency, persistence, boldness, and tool-orientation measured with group experiments. American Journal of Primatology, 75(9), 947–958.
- Mata, R., Frey, R., Richter, D., Schupp, J., & Hertwig, R. (2018).
 Risk preference: A view from psychology. *Journal of Economic Perspectives*, 32(2), 155–172.

- Mata, R., Josef, A. K., & Hertwig, R. (2016). Propensity for risk taking across the life span and around the globe. *Psychological Science*, *27*(2), 231–243.
- McCrae, R. R. (1994). The counterpoint of personality assessment: Self reports and observer ratings. *Assessment*, 1(2), 159–172.
- Muller, M. N., Thompson, M. E., Kahlenberg, S. M., & Wrangham, R. W. (2011). Sexual coercion by male chimpanzees shows that female choice may be more apparent than real. *Behavioral Ecology and Sociobiology*, 65(5), 921–933.
- Newton-Fisher, N. E., Thompson, M. E., Reynolds, V., Boesch, C., & Vigilant, L. (2010). Paternity and social rank in wild chimpanzees (*Pan troglodytes*) from the Budongo Forest, Uganda. *American Journal of Physical Anthropology*, 142(3), 417–428.
- Roberts, B. W., Wood, D., & Smith, J. L. (2005). Evaluating five factor theory and social investment perspectives on personality trait development. *Journal of Research in Personality*, 39(1), 166–184.
- Robson, A. J. (1996). A biological basis for expected and nonexpected utility. *Journal of Economic Theory*, 68(2), 397–424.
- Robson, A. J. (2001). The biological basis of economic behavior. *Journal of Economic Literature*, *39*(1), 11–33.
- Rosati, A. G. (2017). Decisions under uncertainty: Preferences, biases, and choice. In J. Call (Ed.), APA handbook of comparative psychology (Vol. 2, pp. 329–357). American Psychological Association.
- Rosati, A. G., Hagberg, L., Enigk, D. K., Otali, E., Emery Thompson, M., Muller, M. N., & Machanda, Z. P. (2020). Social selectivity in aging wild chimpanzees. *Science*, *370*(6515), 473–476.
- Rosati, A. G., & Hare, B. (2011). Chimpanzees and bonobos distinguish between risk and ambiguity. *Biology Letters*, 7(1), 15–18.
- Rosati, A. G., & Hare, B. (2012). Decision making across social contexts: Competition increases preferences for risk in chimpanzees and bonobos. *Animal Behaviour*, 84(4), 869–879.
- Rosati, A. G., & Hare, B. (2013). Chimpanzees and bonobos exhibit emotional responses to decision outcomes. *PLOS ONE*, 8(5), Article e63058. https://doi.org/10.1371/journal.pone.0063058
- Rosati, A. G., & Hare, B. (2016). Reward currency modulates human risk preferences. *Evolution and Human Behavior*, *37*(2), 159–168.
- Rosati, A. G., Stevens, J. R., Hare, B., & Hauser, M. D. (2007). The evolutionary origins of human patience: Temporal preferences in chimpanzees, bonobos, and human adults. *Current Biology*, *17*(19), 1663–1668.
- Santos, L. R., & Rosati, A. G. (2015). The evolutionary roots of human decision making. *Annual Review of Psychology*, 66, 321–347.
- Schildberg-Hörisch, H. (2018). Are risk preferences stable? *Journal of Economic Perspectives*, 32(2), 135–154.
- Schonberg, T., Fox, C. R., & Poldrack, R. A. (2011). Mind the gap: Bridging economic and naturalistic risk-taking with cognitive neuroscience. *Trends in Cognitive Sciences*, *15*(1), 11–19.

Slovic, P. (1966). Risk-taking in children: Age and sex differences. *Child Development*, *37*(1), 169–176.

- Slovic, P. (1987). Perception of risk. Science, 236(4799), 280–285.Stearns, S. (1992). The evolution of life histories. Oxford University Press.
- Stevens, J. R., Rosati, A. G., Heilbronner, S. R., & Mühlhoff, N. (2011). Waiting for grapes: Expectancy and delayed gratification in bonobos. *International Journal of Comparative Psychology*, 24, 99–111.
- Tan, J., & Hare, B. (2017). Bonobos: Unique in mind, brain and behaviour. Oxford University Press.
- Trautmann, S. T., & van de Kuilen, G. (2015). Ambiguity attitudes. In G. Keren & G. Wu (Eds.), *The Wiley Blackwell bandbook of judgment and decision making* (Vol. 2, pp. 89–116). Wiley-Blackwell.
- Trivers, R. (1972). Parental investment and sexual selection. In B. Campbell (Ed.), *Sexual selection and the descent of man* (pp. 136–179). Routledge.
- Watts, D. P. (2018). Male dominance relationships in an extremely large chimpanzee community at Ngogo, Kibale National Park, Uganda. *Behavior*, 155(13–15), 969–1009.
- Weber, E. U., Blais, A. R., & Betz, N. E. (2002). A domain-specific risk-attitude scale: Measuring risk perceptions and risk behaviors. *Journal of Behavioral Decision Making*, 15(4), 263–290.
- Weiss, A., King, J. E., & Hopkins, W. D. (2007). A crosssetting study of chimpanzee (*Pan troglodytes*) personality

- structure and development: Zoological parks and Yerkes National Primate Research Center. *American Journal of Primatology*, 69(11), 1264–1277.
- Willoughby, T., Heffer, T., Good, M., & Magnacca, C. (2021). Is adolescence a time of heightened risk taking? An overview of types of risk-taking behaviors across age groups. Developmental Review, 61, Article 100980. https://doi.org/10.1016/j.dr.2021.100980
- Wilson, M., & Daly, M. (1985). Competitiveness, risk taking, and violence: The young male syndrome. *Ethology and Sociobiology*, *6*(1), 59–73.
- Wobber, V., & Hare, B. (2011). Psychological health of orphan bonobos and chimpanzees in African sanctuaries. *PLOS ONE*, 6(6), Article e17147. https://doi.org/10.1371/journal.pone.0017147
- Wolf, M., van Doorn, G. S., Leimar, O., & Weissing, F. J. (2007). Life-history trade-offs favour the evolution of animal personalities. *Nature*, 447(7144), 581–584.
- Wroblewski, E. E., Murray, C. M., Keele, B. F., Schumacher-Stankey, J. C., Hahn, B. H., & Pusey, A. E. (2009). Male dominance rank and reproductive success in chimpanzees, Pan troglodytes schweinfurthii. *Animal Behaviour*, 77(4), 873–885.
- Wulff, D. U., Mergenthaler-Canseco, M., & Hertwig, R. (2018).
 A meta-analytic review of two modes of learning and the description-experience gap. *Psychological Bulletin*, 144(2), 140–176.