

A fruit in the hand or two in the bush? Divergent risk preferences in chimpanzees and bonobos

Sarah R. Heilbronner^{1,2,*}, Alexandra G. Rosati^{2,4},
Jeffrey R. Stevens^{5,1}, Brian Hare^{2,3,4}
and Marc D. Hauser^{1,6,7}

¹Department of Psychology, ⁶Department of Organismic and Evolutionary Biology, and ⁷Department of Biological Anthropology, Harvard University, Cambridge, MA 02138, USA

²Center for Cognitive Neuroscience, and ³Department of Biological Anthropology and Anatomy, Duke University, Durham, NC 27708, USA

⁴Max Planck Institute for Evolutionary Anthropology, 04103 Leipzig, Germany

⁵Max Planck Institute for Human Development, 14195 Berlin, Germany

*Author and address for correspondence: B203 LSRC, Research Drive, Duke University, Box 90999, Durham, NC 27708, USA (sarah.heilbronner@duke.edu).

Human and non-human animals tend to avoid risky prospects. If such patterns of economic choice are adaptive, risk preferences should reflect the typical decision-making environments faced by organisms. However, this approach has not been widely used to examine the risk sensitivity in closely related species with different ecologies. Here, we experimentally examined risk-sensitive behaviour in chimpanzees (*Pan troglodytes*) and bonobos (*Pan paniscus*), closely related species whose distinct ecologies are thought to be the major selective force shaping their unique behavioural repertoires. Because chimpanzees exploit riskier food sources in the wild, we predicted that they would exhibit greater tolerance for risk in choices about food. Results confirmed this prediction: chimpanzees significantly preferred the risky option, whereas bonobos preferred the fixed option. These results provide a relatively rare example of risk-prone behaviour in the context of gains and show how ecological pressures can sculpt economic decision making.

Keywords: risk; decision making; chimpanzees; bonobos

1. INTRODUCTION

Animals face risk on a daily basis in contexts ranging from food acquisition to predator avoidance; thus, natural selection probably favours decision mechanisms that cope with this feature of the environment. Numerous studies have established that humans are generally risk averse for gains (preferring a safer option to a risky one) and risk seeking (risk prone) for losses (preferring a risky option to a safe one; Tversky & Kahneman 1981). A wide variety of studies (Kacelnik & Bateson 1996) indicate that

Electronic supplementary material is available at <http://dx.doi.org/10.1098/rsbl.2008.0081> or via <http://journals.royalsociety.org>.

non-human animals show similar patterns of risk sensitivity: species of insects, birds and mammals range from risk neutral to risk averse when making decisions about amounts of food, but are risk seeking towards delays in receiving food. Such strong phylogenetic continuity in economic preferences suggests that these strategies obey a ‘common fundamental principle’ across taxa (Marsh & Kacelnik 2002), representing a generally adaptive strategy for foraging animals.

Animal risk preferences are certainly not, however, invariant—they shift under altered energy budgets and food availability (Caraco 1981; Gilby & Wrangham 2007), as well as when the riskier option is not particularly costly to acquire (Hayden & Platt 2007). This variability implies that animals may adaptively adjust their strategies to local environmental conditions, making ‘ecologically rational’ decisions (Gigerenzer *et al.* 1999). Furthermore, previous studies (Platt *et al.* 1996; Stevens *et al.* 2005a,b) have suggested a relationship between foraging ecology and specific cognitive mechanisms. Nonetheless, we currently have little understanding of whether many of the observed inter-species differences in risk preferences reflect differences in task demands (Macphail 1982), or whether they vary in predictable ways according to species-specific ecological conditions (Harvey & Clutton-Brock 1985). Here, we test the hypothesis that feeding ecology has shaped risk preferences in chimpanzees (*Pan troglodytes*) and bonobos (*Pan paniscus*). Chimpanzees and bonobos are closely related phylogenetically, yet they differ in fundamental ways in their social and foraging behaviours.

Chimpanzees and bonobos diverged from a common ancestor less than one million years ago (Won & Hey 2005). They share many morphological and behavioural characteristics, including body size and appearance, complex multi-male, multi-female societies, and male philopatry (Kano 1992). However, the current research suggests that chimpanzees and bonobos exhibit large differences in dominance structure, sexual behaviour and aggression (Wrangham & Peterson 1996; but see Stanford 1998). As the two species live in geographically distinct areas (Kano 1992; Boesch *et al.* 2002), feeding ecology has been proposed as the major selective force driving these social differences (Wrangham & Pilbeam 2001). Although chimpanzees and bonobos both feed heavily on fruit and engage in ground feeding on terrestrial vegetation, bonobos may rely more heavily than chimpanzees on terrestrial herbaceous vegetation, a more temporally and spatially consistent food source (Wrangham & Peterson 1996). In doing so, bonobos may avoid some of the risk incurred by chimpanzees in their frugivorous foraging. Bonobos may also have access to larger fruit patches, facing less competition within a given patch than chimpanzees (White & Wrangham 1988), potentially turning fruit patches into safer options as well. Furthermore, chimpanzees, unlike bonobos, hunt monkeys, requiring the investment of extensive time into a risky outcome (Gilby & Wrangham 2007). If a group of chimpanzees captures a monkey, the pay-off is high: colobus meat is rich in calories. Thus, hunting probably represents a risky strategy for chimpanzees.

Given that chimpanzees probably cope with more uncertain food sources in their natural environments, we predicted that they would be more risk prone than

Table 1. Individual risk preferences and subject histories. (Chimpanzees were risk seeking, while bonobos were risk averse. The two distributions did not overlap. Asterisk indicates statistical significance.)

subject	proportion fixed choices	<i>p</i> -value	sex	age (years)
<i>chimpanzees</i>				
Fro	0.27	<0.001*	M	12
Pat	0.29	<0.001*	M	8
Pia	0.40	0.035*	F	6
Rob	0.35	=0.001*	M	30
San	0.49	0.79	F	12
<i>bonobos</i>				
Joe	0.69	<0.001*	M	24
Kun	0.71	<0.001*	M	9
Lim	0.63	0.008*	M	10
Uli	0.84	<0.001*	F	12
Yas	0.72	<0.001*	F	8

bonobos in an experimental test of their risk preferences over food. Subjects made a series of choices between one option that always yielded four pieces of food, and another that yielded one piece or seven pieces with equal probability. The expected values of the two options were equivalent, so departures from indifference indicate sensitivity to risk.

2. MATERIAL AND METHODS

We tested five chimpanzees (three males) and five bonobos (three males) at the Wolfgang Koehler Primate Research Center at the Leipzig Zoo, Germany. Subjects were socially housed by species in similar enclosures. All subjects were born in captivity, were never food deprived, had previously participated in cognitive experiments and had ad libitum access to water (including during testing). All subjects received regular daily feedings of fruits, vegetables and roots, and a weekly feeding of cooked meat, a regimen that was not altered during the testing period (electronic supplementary material and table 1).

Subjects experienced three trial types: choice trials, introductory trials and number-discrimination trials. In choice trials, subjects freely chose between the safe and the risky options. In introductory (forced-choice) trials, only one option was present, familiarizing subjects with the reward contingencies. In number-discrimination trials, subjects saw the reward they would receive from both options before making the choice (electronic supplementary material).

Subjects chose between two upside-down bowls that differed in colour and shape (figure 1). The safe bowl always covered four grape halves, and the risky bowl covered one or seven pieces with equal probability; that is, the risky option covered one piece and seven pieces for equal numbers of trials within each session. Subjects made choices by sliding a Plexiglas barrier to one side, giving them access to the options (electronic supplementary material).

After completing number-discrimination and introductory trials, subjects completed six mixed-trial sessions, each consisting of 10 choice trials, four introductory trials and eight number-discrimination trials presented in random order. Subjects then completed three final sessions with 20 choice trials each (electronic supplementary material).

3. RESULTS

In choices between a fixed and a risky reward option (using choice trials from all sessions), chimpanzees were risk seeking (mean \pm s.e. proportion choosing fixed option, 0.36 ± 0.04), significantly preferring the risky reward ($t(4) = -3.48$, $p = 0.025$ one sample *t*-test, all reported comparisons are two-tailed). In contrast, bonobos were risk averse (0.72 ± 0.03), preferring the fixed reward to the risky ($t(4) = 6.40$, $p = 0.003$).



Figure 1. Apparatus. Chimpanzees and bonobos chose between fixed and risky rewards hidden under bowls.

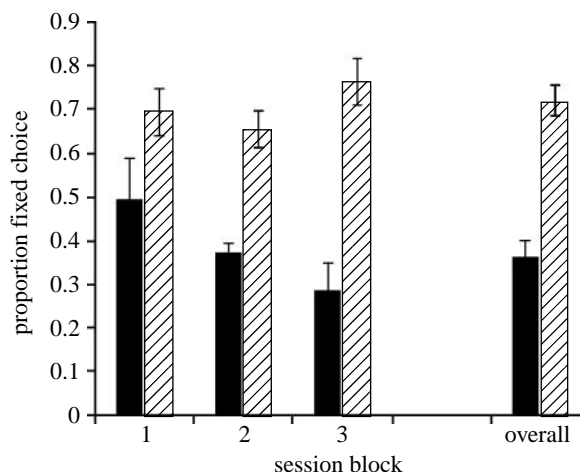


Figure 2. Patterns of risk preferences in apes, across session blocks. Error bars represent standard error. Chimpanzees (black bars) were risk seeking, whereas bonobos (slashed bars) were risk averse. Chimpanzees became slightly more risk seeking as sessions progressed.

Chimpanzees were more risk seeking than bonobos ($t(8) = -6.79$, $p < 0.001$, independent samples *t*-test; figure 2), and binomial tests on individuals' choices revealed that four out of the five chimpanzees exhibited risk proneness, and all bonobos exhibited risk aversion (table 1). The risk preferences exhibited by chimpanzees and bonobos were non-overlapping. There was no effect of sex ($p = 0.37$) or age ($p = 0.82$) on risk preferences (table 1).

A number of alternative explanations could account for these differences. To address differences in learning abilities (the species might have eventually converged on similar preferences), we split the nine sessions into three blocks. A repeated-measures ANOVA with session block as a within-subjects factor and species as a between-subjects factor showed no effect of block ($F_{1,8} = 1.11$, $p = 0.32$). Further, a trend for an interaction between species and block ($F_{1,8} = 4.56$, $p = 0.065$) suggests that the species' preferences

diverged with experience rather than converged (figure 2).

Divergent risk preferences may have stemmed from differences in numerical competence. However, both species were highly successful at choosing the larger reward in the number-discrimination trials dispersed throughout experimental sessions (mean \pm s.e. proportion correct, chimpanzees, 0.95 ± 0.01 ; bonobos, 0.94 ± 0.02 ; $t(8) = 0.38$; $p = 0.71$), suggesting that both species could discriminate the options and were motivated to acquire the larger rewards.

4. DISCUSSION

The chimpanzees and bonobos tested here used disparate strategies when confronted with decisions about risk: chimpanzees preferred risky options and bonobos preferred safe options, an effect that was present in nearly every individual. This difference is notable given that the two species share similar general anatomy and life histories. Our results suggest that species-specific feeding ecologies can strongly influence risk preferences. When compared with bonobos, chimpanzees face riskier foraging situations in their natural habitat and may have therefore evolved more risk-prone decision rules. Note that, although not identical, housing and feeding for the two groups were similar, reducing the likelihood that the observed difference results from these factors. Indeed, the divergent risk preferences of these two species is all the more striking given that they are captive animals housed under similar conditions, suggesting that differences result from evolved decision-making strategies and not prior experience (Burke & Fulham 2003). Nonetheless, although there is substantial overlap in the living conditions and testing environments of our target species, we cannot rule out the possibility that these results are due to the experiences, cultures and conditions of the two specific groups tested here.

The risk-seeking behaviour exhibited by chimpanzees is rarely observed among animals and is likely to be maladaptive in many environments. A forager who reflexively chooses risky options may lose too many gambles to successfully survive. Consequently, the most commonly observed range of risk preferences over gains is indifference or aversion (Kacelnik & Bateson 1996). The chimpanzee strategy, while generally risk prone, may be context specific, lending them flexibility in dealing with their environment. Chimpanzees do show context-specific risk-seeking behaviour by engaging in hunting more often when fruit is plentiful than when it is scarce (Gilby & Wrangham 2007). Overall, the chimpanzees' behaviour demonstrates that risk-proneness may be a more common strategy than usually acknowledged.

Chimpanzee and bonobo risk-sensitive strategies also map directly on to their decisions about delayed rewards. Rosati *et al.* (2007) assessed these apes' temporal preferences by offering subjects' choices between smaller, immediate rewards and larger, delayed rewards. Chimpanzees waited significantly longer than bonobos for the larger rewards. This is particularly relevant for studies of risk because

organisms may perceive delayed rewards as risky. Any number of interruptions could affect the outcome of a future reward, associating the risk-seeking preferences with a preference for a delayed reward. Indeed, our results indicate that the more patient chimpanzees are also more risk prone than bonobos, suggesting that they may wait longer for a delayed reward because they are more willing to incur its associated risk.

Altogether, these findings support growing evidence that decision-making environments shape economic preferences. Though humans systematically violate many of the normative principles of economic theory (Tversky & Kahneman 1981), few researchers have considered preferences in relation to the environment in which they evolved (but see Gigerenzer *et al.* 1999). As humans did not evolve in the context of modern economies, many of our preferences are probably tailored to providing adaptive foraging and other evolutionarily relevant decisions. An evolutionary approach to economic preferences can therefore offer keen insights into the nature of human and animal decision making.

The testing of apes was carried out in accordance with the laws of Germany.

We thank the animal carers of Leipzig Zoo. The research of J.R.S. is supported in part by an NIH National Research Service Award, the research of B.H. is supported by a Sofja Kovalevskaja award from the Alexander von Humboldt Foundation and the German Federal Ministry for Education and Research, and the research of M.D.H. was supported by an NSF Human and Social Dynamics grant, as well as by funds from J. Epstein and S. Shuman.

- Boesch, C., Hohmann, G. & Marchant, L. 2002 *Behavioral diversity in chimpanzees and bonobos*. Cambridge, MA: Cambridge University Press.
- Burke, D. & Fulham, B. J. 2003 An evolved spatial memory bias in a nectar-feeding bird? *Anim. Behav.* **66**, 695–701. (doi:10.1006/anbe.2003.2246)
- Caraco, T. 1981 Energy budgets, risk and foraging preferences in dark-eyed juncos (*Junco hyemalis*). *Behav. Ecol. Sociobiol.* **8**, 213–217. (doi:10.1007/BF00299833)
- Gigerenzer, G., Todd, P. M. & ABC Group 1999 *Simple heuristics that make us smart*. Oxford, UK: Oxford University Press.
- Gilby, I. C. & Wrangham, R. W. 2007 Risk-prone hunting by chimpanzees (*Pan troglodytes schweinfurthii*) increases during periods of high diet quality. *Behav. Ecol. Sociobiol.* **61**, 1771–1779. (doi:10.1007/s00265-007-0410-6)
- Harvey, P. H. & Clutton-Brock, T. H. 1985 Life history variation in primates. *Evolution* **39**, 559–581. (doi:10.2307/2408653)
- Hayden, B. Y. & Platt, M. L. 2007 Temporal discounting predicts risk sensitivity in rhesus macaques. *Curr. Biol.* **17**, 49–53. (doi:10.1016/j.cub.2006.10.055)
- Kacelnik, A. & Bateson, M. 1996 Risky theories: the effects of variance on foraging decisions. *Am. Zool.* **36**, 402–434. (doi:10.1093/icb/36.4.402)
- Kano, T. 1992 *The last ape*. Stanford, CA: Stanford University Press.
- Macphail, E. M. 1982 *Brain and intelligence in vertebrates*. Oxford, UK: Clarendon Press.

- Marsh, B. & Kacelnik, A. 2002 Framing effects and risky decisions in starlings. *Proc. Natl Acad. Sci. USA* **99**, 3352–3355. (doi:10.1073/pnas.042491999)
- Platt, M. L., Brannon, E. M., Briese, T. L. & French, J. A. 1996 Differences in feeding ecology predict differences in performance between golden lion tamarins (*Leontopithecus rosalia*) and Wied's marmosets (*Callithrix kuhli*) on spatial and visual memory tasks. *Anim. Learn. Behav.* **24**, 384–393.
- Rosati, A. G., Stevens, J. R., Hare, B. & Hauser, M. D. 2007 The evolutionary origins of human patience: temporal preferences in chimpanzees, bonobos, and adult humans. *Curr. Biol.* **17**, 1663–1668. (doi:10.1016/j.cub.2007.08.033)
- Stanford, C. B. 1998 The social behavior of chimpanzees and bonobos: empirical evidence and shifting assumptions. *Curr. Anthropol.* **39**, 399–420. (doi:10.1086/204757)
- Stevens, J. R., Hallinan, E. V. & Hauser, M. D. 2005a The ecology and evolution of patience in two New World monkeys. *Biol. Lett.* **1**, 223–226. (doi:10.1098/rsbl.2004.0285)
- Stevens, J. R., Rosati, A. G., Ross, K. R. & Hauser, M. D. 2005b Will travel for food: spatial discounting in two New World monkeys. *Curr. Biol.* **15**, 1855–1860. (doi:10.1016/j.cub.2005.09.016)
- Tversky, A. & Kahneman, D. 1981 The framing of decisions and the psychology of choice. *Science* **211**, 453–459. (doi:10.1126/science.7455683)
- White, F. J. & Wrangham, R. W. 1988 Feeding competition and patch size in the chimpanzee species *Pan paniscus* and *Pan troglodytes*. *Behaviour* **105**, 148–164.
- Won, Y. J. & Hey, J. 2005 Divergence population genetics of chimpanzees. *Mol. Biol. Evol.* **22**, 297–307. (doi:10.1093/molbev/msi017)
- Wrangham, R. W. & Peterson, D. 1996 *Demonic males: apes and the origins of human violence*. Cambridge, MA: Harvard University Press.
- Wrangham, R. W. & Pilbeam, D. 2001 African apes as time machines. In *All apes great and small* (eds B. M. F. Galdikas, N. E. Briggs, L. K. Sheeran, G. L. Shapiro & J. Goodall), pp. 5–17. New York, NY: Kluwer Academic/Plenum.