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

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Abstract

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 behavior 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 behavioral 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 behavior 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 favors 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 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 behaviors.

Chimpanzees and bonobos diverged from a common ancestor less than one million years ago (Won & Hey 2005). They share many morphological and behavioral 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 behavior 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 bonobos in an experi-

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	p-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

mental 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 color 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 (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 (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 ($t(4)=6.40$, $p = 0.003$). Chimpanzees



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

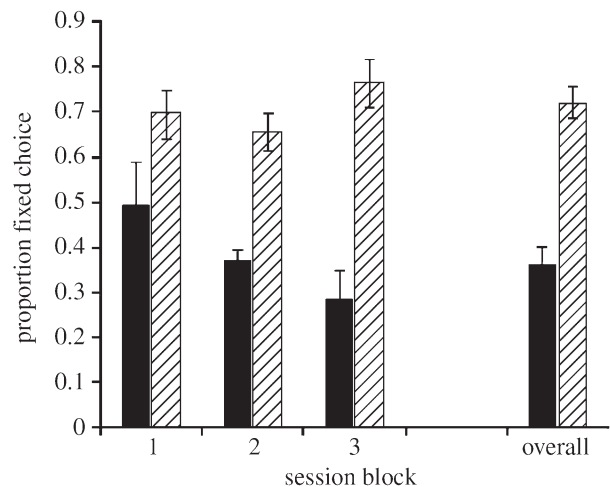


Figure 2. Patterns of risk preferences in apes, across session blocks. Error bars represent standard error. Chimpanzees (black bars) were risk seeking, whereas bonobos (slashed bars) were risk averse. Chimpanzees became slightly more risk seeking as sessions progressed.

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 ($F_{1,8} = 4.56$, $p = 0.065$) sug-

gests 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 behavior 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 behavior by engaging in hunting more often when fruit is plentiful than when it is scarce (Gilby & Wrangham 2007). Overall, the chimpanzees' behavior 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.

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Supplementary Material follows References.

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Supplementary Material

Methods

Subjects

We tested five bonobos (three males: Kuno, Limbuko, and Joey; two females: Yasa, Ulindi) and five Western common chimpanzees (three males: Patrick, Robert, and Frodo; two females: Sandra and Pia). While subjects were not perfectly matched in age, there was no systematic age difference between the two groups (see Table 1).

Chimpanzee subjects were all part of a 17-member social group, one of two separately housed chimpanzee groups at the zoo. Bonobo subjects were all part of a six-member social group (the sixth, untested bonobo is an infant female). During the day, each group had access to both a smaller, indoor enclosure and a larger, outdoor enclosure, subject to the time and the weather. At night, they slept in group-specific indoor rooms, and both species made the transfer into and out of this room at approximately the same time. Chimpanzee and bonobo subjects both experienced regular enrichment, including foraging-specific enrichment. All had unrestricted access to water, even during testing. Subjects were tested between the hours of 08:30 and 12:30, with no subject's testing locked to a particular time within that frame. All subjects were born in captivity, were never food-deprived, and could stop participating at any time. While housing and rearing conditions for the two species were certainly not identical, they were quite similar, and were certainly much more alike than those experienced by these animals in the wild. In particular, the feeding regimens (highly relevant to these food-based choice tasks) for the two groups were essentially the same. Thus, observed differences between the two groups are much more likely to be due to their evolutionary histories than differences in housing, although the latter is still a distinct possibility.

Apparatus

Subjects faced the experimenter through a Plexiglas panel with holes on either side through which subjects could reach to make choices by sliding a small Plexiglas barrier (60 cm long and 9 cm tall) to one side, uncovering the hole in front of that bowl. This barrier was used to prevent subjects from choosing both options, as sliding the barrier to one side blocked the opposite hole. Food rewards were placed on a plastic 73 cm × 33 cm table attachment. Rewards were obscured by plastic colored bowls (diameter = 26 cm, height = 12 cm) and a 70 cm × 27 cm × 23 cm occluder. This occluder was used to cover the bowls during baiting to ensure that subjects did not know how many items were available beneath the risky option. During sessions, the experimenter placed the options on a table (73 cm × 33 cm) that could be slid forward within the subject's reach. The side assignments for the options were counterbalanced within sessions.

Trial Structures

Both chimpanzees and bonobos chose between a safe reward (associated with a particular bowl shape and color) that always yielded four grape halves and a risky reward (under the other colored bowl) that yielded seven grape halves 50% of the time and one grape half the other 50% of trials. For all trial types, the inter-trial interval (time between end of one trial and beginning of another) was set at approximately 25 s. During the inter-trial interval, the experimenter loaded the table with the appropriate food rewards and covered each side with a colored bowl. We counterbalanced the assignment of bowl color to option type (fixed versus risky) across subjects. All loading occurred behind an occluder. Reward options were randomized across trials. The experimenter always loaded the rewards from left to right, in case subjects attempted to infer amounts from body placement. At the end of the inter-trial interval, the trial began when the occluder was lifted. In choice trials, the subject then saw the two options for 4 s prior to making a choice. In introductory trials, only one option was available to choose. In number-discrimination trials, subjects saw the actual reward quantities for 4 s before the experimenter then covered them with the appropriate bowls in view of the subject. When the 4 s had passed, the experimenter pushed the table forward to allow the subject to make a choice. The subject then had 15 s to make a choice by sliding the Plexiglas barrier to one side. The experimenter then uncovered the food amount beneath the chosen bowl and handed it to the subject.

Discarding Data

If a subject did not make a choice (meaning did not slide the Plexiglas barrier to one side) within 15 s of being given access to the barrier, the trial was considered aborted. Additionally, if a subject failed to consume all the food, the trial was aborted. Aborted trials were appended to the end of the session. However, upon three aborted trials in a single session, the entire session was ended and the data discarded. Only one session had to be aborted in this way.

Criteria were also established to eliminate severely side-biased data. For mixed sessions, if a subject chose a single side nine or more times out of ten possible choice trials in a single session, plus chose incorrectly toward the side of the bias on a single number trial, the data from that session was discarded and the session repeated. For the later, choice sessions, if a subject chose a particular side on 18 out of 20 trials or more,

that data was discarded and the session repeated. Only a single session was deemed biased based on these criteria, suggesting that the apes found the task and the reward contingencies highly salient.

Pretest Sessions

Prior to beginning the experimental sessions, all subjects completed two types of sessions: number-discrimination and introductory sessions. During the number-discrimination session, there were 20 number-discrimination trials, 10 of each comparison type. In order to progress to the introductory session, each subject had to choose the larger reward on 8 of 10 trials for each comparison type. Subjects repeated number-discrimination sessions until they reached this threshold. During the introductory session, subjects only had one possible option available to them. Of the 20 trials in an introductory session, 10 presented the risky option (split between one and seven rewards) and the other 10 presented the fixed option. In order to proceed from the introductory session to the mixed sessions, subjects had to choose the side with a reward available on 19 of 20 trials.

Results

A Shapiro-Wilks W test revealed that the data were not violating assumptions of normality, $W = 0.952$, $p = 0.753$ (chimpanzees), $W = 0.898$, $p = 0.399$, bonobos. The Levene's Test for Equality of Variances confirmed that the two data sets were sufficiently homogeneous, $p = 0.56$.

To determine whether this pattern could be attributed to species or individual differences in numerical discrimination, subjects also completed number-discrimination choices over the relevant quantities. Chimpanzees and bonobos did not differ in the number of sessions it took to reach criterion for discrimination, $t(8) = 0.426$, $p = 0.68$ (Levene's Test: $p = 0.53$), or on their overall performance on the number-discrimination

trials dispersed through the first six experimental sessions, $t(8) = .381$, $p = .71$ (Levene's Test: $p = .554$). Furthermore, individual differences in number discrimination performance did not predict their risk preferences, $r = -.013$, $p = 0.73$, Pearson correlation. One additional possibility is that the chimpanzees and bonobos differed in their motivation to acquire the food. Three pieces of evidence suggest that this is not the case. First, chimpanzees and bonobos received equal amounts of food in the task overall despite their different choice strategies. Second, both species were highly successful at picking the larger reward on the number-discrimination trials, suggesting similar levels of engagement in the task. More importantly, if one of the species was unmotivated to acquire the food, then that species might have performed at chance in the choice trials due to lack of interest. Thus, differences in motivation cannot account for the strong, but divergent, preferences that both species exhibited.

The amount received from the risky reward in experimental choices could vary slightly from session to session and between individuals; however, on both an individual and group level, subjects did not receive the larger or smaller reward from the risky option more often than chance, $t(9) = -1.37$, $p = 0.20$ (group-level analysis). In addition, these variations did not affect subjects' choices, $r = 0.157$, $p = 0.67$, and there was no difference between species in overall amount received, $t(8) = -0.114$, $p = 0.89$ (Levene's Test: $p = 0.23$). This precludes the possibility that the observed differences resulted from different reward amounts received rather than risk preferences.

An analysis of first-order transitions (run on the last three sessions only – this being the explicit reason for running the choice sessions) revealed that, on both individual and group levels, subjects were not more or less likely to switch to the fixed reward directly after receiving the small payoff from the risky reward than after receiving the large payoff, $t(9) = 1.527$, $p = 0.161$, two-tailed paired-samples t -test.

