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Risk sensitivity, phylogenetic reconstruction, and four chimpanzees

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Abstract

Sensitivity to variance, or risk, has been considered elementary to economic decision making, featured prominently in discussions of primate species-typical behaviors and phylogeny, and heralded as a challenge to deterministic foraging theory. Most risk sensitivity studies involve dichotomous choices and small spatial scales, providing only limited bases for predicting how variance information might be used across contexts. We examined foraging risk-sensitivity in four chimpanzees (*Pan troglodytes*) which were presented containers associated with particular mean food rewards/variances. Preferences were measured via indoor dichotomous choice tests. Subsequent tasks, designed to assess how well these preferences held up across situations, involved a differing food type, rank-ordering arrays of containers, and/or recovering them in a large outdoor testing area. In addition, some variations involved memory for containers previously observed being hidden. Risk preferences varied by subject, experimental context, reward type, and mean reward quantity. In rank-ordering experiments, under the reward contingencies utilized, mean food quantity was a better predictor of selection order than variance. These results bring into question arguments that species-typical primate risk traits—in the sense of enduring, generalized dispositional features of organisms—have been firmly identified, and suggest that many popular experimental strategies are alone inadequate for reconstructing risk-related traits in primate/human evolution. Models from classical foraging theory, which do not address variance, have likely been successful because they include crucial variables with robust predictive value. Determining the importance of variance to naturalistic decision-making, on the other hand, will require further testing in a wide range of experimental and observational contexts.

Keywords

variance sensitive foraging; primate cognition; primate evolution; human evolution; memory; optimal foraging theory

Life is uncertain. Eat dessert first.

Ernestine Ulmer (in Byrne 2012)

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All methods were approved by the Institutional Animal Care and Use Committee (IACUC) of Georgia State University. Participation was voluntary on the part of the chimpanzees.

Introduction

Parasites, disease, crimson teeth and claws, natural disasters—yes, the world is a place where uncertainty would seem to rule. And, as traditional wisdom tells us, there is not even respite from this unpredictability while eating. To a forager in nature, resources come in a wide array of packages, and variance, or risk, has long been considered an essential variable in economic decision making. It has also widely been considered to present a challenge to assumptions from classical foraging theory, such as the touchstone optimal diet model, which does not take into account the variance associated with food item values, handling times, or encounter rates (Schoener 1971; Charnov 1976; Caraco et al. 1980; Kacelnik and Bateson 1996).

To experimentalists in laboratory and field settings, the question of “risk sensitivity” has generally been approached using a deceptively simple paradigm. An animal is given a choice between two options or option types—whether they be visible containers, levers, or distinctive food wells—which commonly are equivalent in mean utility (e.g., food quantity, delay to reward, net energy intake) but differ in their respective variances. For example, a rhesus monkey might choose between displacing a “stable” object that always covers one popcorn kernel or a “variable” (or “risky”) object that covers 0 or 2 kernels with equal probability (Behar 1961, which predates risk-sensitive foraging theory but utilizes its later methodology).

Such classic tests share a number of features, all important to their interpretation. For one, the options—absolutely two, or more than two categorized into two distinct “types”—are close to each other in space and time and thus represent “simultaneous encounters” in the parlance of foraging theory (Engen and Stenseth 1984). In addition, the options are visible and correlated with set average values and variances, and the animal cannot obtain any further information about the available rewards until it actually exploits an option. In the rhesus monkey example, for instance, whether a variable object covered 0 or 2 popcorn kernels was unknown until that object was displaced. Although the conditions of “dichotomous choice,” “simultaneous encounters,” “visible options,” and “no further information pickup” have facilitated these studies, it is fair to ask how commonly such situations occur collectively in nature, and how, and to what degree, natural selection can act on the psychological mechanisms which lead to observed experimental outcomes.

Many factors can potentially influence whether a particular animal exhibits experimental risk sensitivity, and, if so, in what direction. For example, many taxa show risk-aversion or indifference with respect to variability in reward amount, but risk-proneness with respect to variability in delay to reward (Kacelnik and Bateson 1996, 1997). Exceptions, however, are numerous, particularly with respect to amount, and risk preferences can vary or change based on individual energy balance, ambient temperature (especially in small animals such as juncos, Caraco 1981; Caraco et al. 1990; Lim et al. 2015), colony-level energetic considerations (e.g., bumblebees, Cartar and Dill 1990), and other factors.

Although risk or variability has long been of interest in the study of human decision making (Markowitz 1952), up until recently it had only infrequently been considered in nonhuman

primates. A rectification has begun, with multiple studies over the last decade utilizing variants of the classical paradigm where nonhuman primates needed to learn the means and variances of single reward types (Table 1). Risk has also been examined in other ways, such as having the subjects choose between a safe food of intermediate value and a variable option that provides a low value food or high value food with known probability (Rosati and Hare 2011, 2012).

Much more so than with other taxa, work in primate risk-sensitivity has commonly been conducted with phylogenetic aims, such as identifying risk-preferences for individual species, or groups of species. Lemurs as a whole, for example, have been described as risk-averse (MacLean et al. 2012). Chimpanzees have been categorized as risk-prone, in contrast to their putatively risk-averse sister taxon, the bonobo (Heilbrunner et al. 2008). The explanatory hypotheses for such results are frequently ecological; e.g., lemurs live in unpredictable Malagasy habitats, and have possibly evolved to take sure bets when they can find them (MacLean et al. 2012) and chimpanzees are commonly thought to engage in “risky” foraging behaviors, such as the hunting of vertebrates, more often than bonobos (Heilbrunner et al. 2008; but see Hohmann and Fruth 2007). In some cases, the phylogenetic aims or claims are more ambitious; for example, it has been suggested that risk-sensitivity studies in apes “illuminate the evolutionary roots of human economic behavior” (Rosati and Hare 2011, p. 15) and provide evidence of “self-domestication” in bonobos (Hare et al. 2012), a process sometimes invoked to describe important aspects of human behavioral evolution (Lorenz 1954/1971).

These phylogenetic interpretations are based on only a few studies and are necessarily provisional. As in other animals (Kacelnik and Bateson 1996), primate risk preferences are not fixed, and can vary across individuals of the same species or across situations in a single individual. For example, rhesus monkey responses to variance differed between experienced (risk-averse) and naïve (risk-neutral) participants in a tray testing paradigm (Behar 1961) and shifted from risk-proneness to risk-neutrality in a computer testing regime when intertrial intervals were increased (Hayden and Platt 2007). Similarly, chimpanzee and bonobos shifted their preferences—in one case, towards increasingly risky choices—when tested in a social context as opposed to an asocial one (Rosati and Hare 2012; cf. Giraldeau and Caraco 2000).

In addition, natural primate foraging behavior, perhaps more so than in any animal group, is likely to deviate from the situation envisioned in a traditional risk-sensitive foraging experiment. As opposed to making choices over a computer screen or testing tray, wild primates exploit widely scattered resources and make decisions over expansive spatial and temporal scales (Menzel 1997; Dolins and Mitchell 2010). Most primates have broad diets, and in all likelihood must choose daily from among potential resources differing in type, patch size, energetic value, expected pursuit and processing time, and predation danger (Harding 1981; Lambert 2010; Sayers et al. 2010; Sayers 2013; Sayers and Lovejoy 2014).

There is also a growing body of evidence that primates can take into account the location and nature of resources that are outside sensory range (e.g., Garber 1989; Menzel 1991, 1999; Cunningham and Janson 2007; Janmaat et al. 2014; Noser and Byrne 2015). Decisions

about which food patches to exploit might be made long before the resources are “encountered” in the traditional sense (Waddington and Holden 1979; Engen and Stenseth 1984; Stephens and Krebs 1986) of being detected by vision, smell, or other direct modality. Simultaneous encounters of visible, dichotomous options are but a small subset of the choice problems faced by wild primates, and some primates, if not all of them, may routinely compare nearby resources with more distant ones by memory (Sayers and Menzel 2012). Additionally, and in common with many other animals, primates can in some cases gather information by visually inspecting patches before entering them, reducing uncertainty (Menzel 1991; Dominy et al. 2001). Thus, to the extent that primates consider variance in making foraging decisions, they are constantly weighing this against many other variables. At present, we know little of how variance preferences change across different food types or quantities, or over large spatial scales, or when more than two discrete options or option types are available.

In this study, we conducted a series of experiments with chimpanzees (*Pan troglodytes*) designed to determine to what degree previous findings on risk sensitivity in this species could be generalized to differing food types, quantities, and experimental formats, as well as to identify whether any of our four chimpanzee subjects could integrate mean quantity and variance information in rank-ordering tasks with more than two options available. A subset of the rank-ordering experiments were performed in an outdoor testing area, and in a further subset the apes “recovered” test items previously observed being hidden (by directing a naïve human to their locations)—and thus involved the type of memory widely thought to be important in wild primate foraging. Behavior was analyzed at the level of individual apes, which were not treated as group-collated “stand-ins” for their entire species.

The experiments were not designed to be strict simulations of natural feeding behavior, but rather represented conditions intermediate between laboratory and field, involving certain situations with greater complexity and/or larger spatial scales than in standard risk sensitivity studies. More general aims were to evaluate, in light of the findings, prior interpretations of nonhuman primate risk sensitivity, as well as phylogenetic extensions from this work, and to discuss the relevance of risk to classical foraging theory.

Material and methods

Subjects and environment

The subjects were four chimpanzees at the Language Research Center, Georgia State University. These included females Lana (age 39) and Panzee (age 24) and the males Mercury (age 23) and Sherman (age 36). All four apes had long been involved in psychological testing, and all excepting Mercury were proficient in the use of lexigrams—arbitrarily designated visuo-graphic forms that stood for items, locations, individuals, and events (Rumbaugh and Washburn 2003). Except where stated otherwise, all four chimpanzees participated in each of the experiments described here.

The chimpanzee were housed in a building with four indoor cages, the location of indoor testing, and three outdoor enclosures. A wooded area contiguous to the outdoor enclosures (approximately 350 m²) served as the location for outdoor testing. The chimpanzees could

not enter the woodland, but could view it from fenced towers located in the outdoor enclosures. Chimpanzees had daily access to both the indoor cages and outdoor enclosure and could move freely between them. The apes received three meals of fruits and vegetables daily. Those with requisite training could request specific foods via lexigram, and none were food or water deprived for testing, which was conducted in the afternoon, generally beginning 1–2 hours after the chimpanzees' midday meal. It is thus likely the chimpanzees were on positive energy budgets (Caraco 1981) throughout the course of this experiment.

Note on blinded methods

This study involved the selection of goal objects by chimpanzees. To reduce observer bias, the individuals (caretakers) recording ape choices, in all experiments, were blind to the contents of goal objects, as well as to the aims of the experiment and overall project. In some experiments where the goal objects were hidden, the caretakers were additionally blind to the location of goal objects. In addition, steps were taken to reduce or eliminate the possibility of unintentionally cueing the animals in favor of any particular selection (details below).

General methods – indoor testing

All indoor testing was performed on a sliding tray which could be withdrawn behind or pushed in front of an opaque blind. The blind could be raised and lowered by the experimenter, who was seated on one side of the blind, with the ape (in its indoor enclosure) on the other. Test items were placed on the tray by the experimenter and, where applicable, multiple containers were located approximately 40 cm from each other. Left-right placement (for dichotomous choice trials) or relative L-R position on the tray (for rank-ordering trials) were determined for each trial by random computer draw before each session. Where applicable, the contents of “variable” containers (see below) were determined pseudo-randomly, with the provision that variable positive and variable negative (zero-level) rewards appeared an equal number of times per session and/or over all sessions.

The experimenter then partially lifted the blind, keeping his face hidden from the ape, and pushed the tray forward towards the ape. The chimpanzee made its selection by extending its finger through the wire mesh and touching the tray next to one of the containers, and the selection was announced by a caretaker located peripheral to the ape. The caretaker was naïve to the contents of containers or the goals of the study. The caretaker opened the container, and any contents were given by him or her to the subject. The experimenter then lowered the blind in preparation for the next trial (dichotomous choice) or next presentation (rank-ordering, which allowed the ape to select one container per round of choice, without replacement, and which continued until all choices were exhausted). Intersession intervals were 16 hours, and intertrial intervals within session were 2 minutes.

General methods – outdoor testing

Each outdoor trial consisted of a cue-giving phase, a delay phase, and a response phase. In the cue-giving phase, the experimenter stood in the wooded area outside a chimpanzee's outdoor enclosure. On the ground, next to the experimenter, was an opaque box containing the test items (containers) for that trial. The chimpanzee looked on from the other side of the

fence, inside the tower of the outdoor enclosure. The experimenter removed the first test item from the box, held it up approximately 1 m from the chimpanzee for 5 seconds, and then either placed it visible on the ground, or hid it in the test area, depending on the experiment. “Hiding” consisted of digging a hole within visual range of the ape, placing the container within it, and then covering the container with soil and leaves, leaving the ground surface appearing undisturbed. This was then repeated with the remaining test items. In experiments in which containers were hidden, the chimpanzee saw only one container at a time. The order in which test items were shown, and the location in which they were to be placed or hidden, was determined by random computer draw before each trial.

In most experiments, the trial-specific distances from the tower at which items were placed or hidden were kept approximately constant (generally, they were equal to within ± 1 m), on an invisible “arc” from the subject (“distance controlled”). All four chimpanzees participated in the “distance controlled” experiments. For Lana, items were always placed or hidden on an arc within 2 m of the tower, and for the other apes (who had more experience directing to more remote targets, see below) the arc was situated at any distance up to approximately 20 m. In one experiment, however, the within-trial distances between the chimpanzee and individual containers were drawn pseudo-randomly from all distances up to 20 meters; i.e., containers might be located at substantially differing distances from the subject (“distance free to vary”). Mercury, Panzee, and Sherman participated in the “distance free to vary” experiment.

After all test items for a trial had been placed or hidden, the experimenter left the scene. There was then a delay interval of 15 minutes before the subjects could initiate response. The response phase consisted of the chimpanzee “recruiting” an experimentally naïve human caregiver indoors and prompting him or her to go outside to the test area. This person was unaware of what was placed or hidden, or where. Recruitment typically involved, on the part of the chimpanzee, vocalizations, lexigram use, and/or pointing to the tunnel leading to the outdoor enclosure adjacent to the test area (Menzel 1999; Putney 2007).

Once the person was outside in the test area, and the chimpanzee was in the adjacent tower of the outdoor enclosure, the ape directed the person—via manual and bodily pointing, other gesture, and vocalization—to particular containers or search locations. An advantage of this method is that the costs of locomotion are essentially removed, allowing tradeoffs (such as between mean reward and variance) to be examined in a relatively simple manner (Sayers and Menzel 2012). All of the apes had previous experience directing humans to items and search locations, and over the distances utilized. If a test item was selected (visible trials) or uncovered (hidden trials) by the person during a search, it was opened and its contents were given to the ape. Searches, unless otherwise noted, continued until the chimpanzee terminated the trial by leaving the tower of the outdoor enclosure. Further information on this testing method is given elsewhere (Menzel 2005, 2012; Menzel and Menzel 2012; Sayers and Menzel 2012; Roberts et al. 2014).

After the response phase ended, the locations of unsuccessful searches were recorded on a map of the test area. Any search within 61 cm (exactly 24 inches) of an item was considered

a recovery of that item. Given that the test area is large (~ 350 m²), this was a very small margin for error. Intertrial intervals were 16 hours.

Data analyses

Data from individual chimpanzees were analyzed separately, and descriptive statistics were compiled for all experiments. Dichotomous choice data were analyzed via binomial tests. Rank-ordering data were analyzed by general linear model ANOVA with order selected as the dependent variable and mean quantity (4 and 16) and stable-variable (scored 1–2) as fixed factors. Partial eta squared was calculated as an estimate of effect size for mean quantity, variance, and the interaction between these factors. Possible relationships between recovery order and “distance from subject,” in the experiment where distance was free to vary, were assessed by Friedman Analysis of Variance by Ranks. In cases where significant Friedman results were obtained, Spearman rho correlations were calculated for recovery order and distance for each individual trial, and a mean rho was computed. Alpha level was set at 0.05.

Sequence of experiments

The experiments, and variations within each experiment, were performed in the order given below unless noted otherwise.

Experiment 1: Quantity and risk preferences for a peanut reward on an indoor testing tray—The purpose of this experiment was to: 1) assess individual chimpanzee risk preferences with a peanut reward (two different mean quantities, each with two variance levels), indoors, on a testing tray, and 2) to evaluate whether the apes would retain any variance preferences, and efficiently incorporate the available information on mean quantities, when subsequently presented with all four test items simultaneously on the tray in a 1-2-3-4 rank-ordering task—i.e., would the apes select larger mean quantities before smaller ones, and/or consistently favor stable or variable containers?

Experience with containers: All chimpanzees were given experience with arbitrary visual signs of food—four unique opaque containers, with distinctive mean quantities and variances of peanuts, a moderately preferred food. The containers differed in shape and color but were approximately equivalent in volume. The containers included: 1) *stable 4* (a blue plastic cylinder measuring 16.25 cm height × 8 cm basal diameter), which always held 4 peanuts, 2) *variable 4* (a yellow plastic container, 13.25 cm height × 10 cm width × 6 cm depth), which held either 0 or 8 peanuts with a 0.5 probability of each, 3) *stable 16* (a white plastic cylinder, 19 cm height × 7.5 cm basal diameter), which always held 16 peanuts, and 4) *variable 16* (a silver aluminum cylinder with plastic top, 14 cm height × 10 cm basal diameter), which held either 0 or 32 peanuts with a 0.5 probability of each. Peanuts within containers were sealed in a clear plastic bag; we put empty plastic bags in containers that had no peanuts.

All chimpanzees participated in introductory and mixed sessions to allow familiarization with the containers and their associated rewards (modified from Heilbronner et al. 2008). In introductory sessions, only one container was available on the tray per trial, and only one

mean quantity was presented (either 4 or 16). Each subject completed 4 sessions of 12 trials apiece for each mean quantity (48 trials/mean quantity; 96 trials total). During each introductory session, the stable and variable containers each appeared 6 times; variable positive (i.e., 8 or 32) and variable negative (i.e., 0 or 0) each appeared 3 times. We then conducted four mixed sessions for each mean quantity. Each consisted of 6 dichotomous choice trials and 4 introductory trials. In each dichotomous choice trial, the stable container and the variable container for the same mean quantity were available simultaneously on the tray. In each introductory trial in the mixed sessions, as in the introductory sessions, one container was available (2 trials with the stable container, 1 with variable positive, 1 with variable negative).

Experiment 1a - Dichotomous choice test—This experiment represented a standard, dichotomous choice risk sensitivity test. Experimental sessions, for each mean quantity of peanuts (4 and 16), consisted of 10 dichotomous choice sessions of 10 trials apiece ($n = 100$ trials/mean quantity/chimpanzee). In each dichotomous choice trial the stable container and the variable containers for a given mean quantity were available simultaneously. We alternated the two mean quantities in blocks of two sessions (i.e., two sessions of mean quantity 4, followed by two sessions of mean quantity 16, then two sessions of mean quantity 4, and so on).

Results: For mean quantity 4 peanuts, two chimpanzees (Lana, Mercury) preferred the “risk-prone” or variable container, while the other two apes (Panzee, Sherman) were “risk-neutral” or indifferent to variance (Table 2). For mean quantity 16 peanuts, all four chimpanzees preferred the variable option. Thus, in a classic-style variance sensitive foraging assessment with a standard laboratory reward, the chimpanzees were risk-prone when they showed any preference, similar to previous studies (Heilbronner et al. 2008; Haun et al. 2011). Two subjects, however, varyingly displayed risk neutrality or proneness dependent on differences in mean quantity.

Experiment 1b - Rank-ordering test—To examine the stability of tray preferences, and the ability of the chimpanzees to combine different kinds of information, this experiment considered whether individual apes would utilize mean quantity and variance associations from the previous experiment in a *series* of choices. All four containers (stable 4, variable 4, stable 16, variable 16) were available on the tray simultaneously, and selection continued one container at a time, without replacement, until all containers were exhausted. Each rank-ordering trial thus consisted of 4 successive choices. Trial 1 of this variant was the first time each subject had observed all the containers at the same time. Experiment 1b consisted of 12 sessions with 4 trials apiece ($n = 48$ trials/chimpanzee).

Results: For all chimpanzees, the 1-2-3-4 order in which containers were selected was significantly related to both the mean quantity and variance associated with containers, with the effect size for mean quantity being greater (Table 3; Fig. 1). All apes selected containers that had means of 16 peanuts before those with means of four and selected the variable 16 container before the stable 16 container. Lana also selected the variable 4 container before the stable 4 container. For the other subjects, there was a significant interaction between

mean quantity and variance. Mercury distinguished the containers with means of four less sharply than those with means of 16 (with variable 4 again being selected earlier than stable 4 on average); Panzee and Sherman did not distinguish between the mean 4 containers. Taken together, the results for individual chimpanzees were generally similar to those of Experiment 1a, with the addition that the containers paired with the larger mean quantity were on average selected before those with the smaller mean quantity, and that the effect size for quantity, over these reward contingencies, dwarfed that of variance.

Experiment 2: Quantity and risk preferences for a peanut reward in an outdoor testing area—The purpose of this experiment was to: 1) determine whether individual chimpanzees would maintain any preferences exhibited in Experiment 1 in an outdoor context, 2) assess chimpanzees' memory for the same containers, as reflected in their rank-order recovery after being hidden, and 3) evaluate the relative influence of mean quantity and variance on recovery order. Items hidden or placed during cue giving included all four containers from Experiment 1.

Experiment 2a – Containers hidden, distance free to vary (20 trials/ chimpanzee)—We showed previously (Sayers and Menzel 2012) that food type, food quantity, and how far chimpanzees were from containers they had seen hidden influenced the order in which they selected them. Thus, we designed experiment 2a to determine whether the subjects in this study would take into account variance when making similar selections. Each container (peanut reward; stable 4, variable 4, stable 16, variable 16) was hidden in a random location 20 m from the chimpanzee. The distance within this range was considered “free to vary” (randomly selected) to gauge its effect, if any, on recovery order. After a minimum 15 minutes delay, the ape directed a naïve caregiver to search locations, and the contents of containers, if and when recovered, were given to the subject. Mercury, Panzee, and Sherman participated in this experiment; Lana, who had less previous experience directing to locations/objects greater than 2 m distant, was excluded.

Results: For Mercury and Sherman, the mean quantity associated with containers was significantly related to recovery order, but variance was not (Table 4, Fig. 2). Larger mean quantities were on average recovered before smaller quantities. The distance items were hidden from the subject was not significantly related to recovery order for either of these apes (Friedman tests, $n = 20$, $df = 3$, all p 's > 0.21). The order in which items were selected by Panzee was not significantly related to either mean quantity or variance. A significant interaction between mean quantity and variance was detected only for Panzee (Table 4, Fig. 2). For this ape, however, the distance items were hidden from the subject was significantly related to recovery order (Friedman Chi Square = 14.16, $n = 20$, $df = 3$, $p = 0.003$). Closer containers were on average recovered sooner; the Spearman rho between recovery order and distance for individual trials had a positive sign for 15 trials, a negative sign for two, and a zero sign for three; mean rho = 0.42. Thus, two chimpanzees transferred information on at least mean quantities to the outdoor setting and used this to guide their recovery orders of containers previously observed being hidden. In contrast, variance was not significantly associated with selection order for any of the subjects.

Experiment 2b – Containers visible, distance controlled (20 trials/chimpanzee).—In the previous experiment, Panzee relied on a simple “distance-away” heuristic and did not use information on mean quantity or variance. Experiment 2b simplified the problem by controlling for distance and having the containers visible. This was an outdoor version of Experiment 1b, with the additions of: 1) a minimum 15 minute delay between when the chimpanzee first observed the containers and when she or he could make selections, 2) a much longer intertrial interval (16 hours), and 3) containers that were further spaced from the subject, and each other.

Containers (peanut reward; stable 4, variable 4, stable 16, variable 16) were placed in pseudo-random locations on an arc around the chimpanzee’s outdoor tower. The left-right position of items around the arc was randomized across trials. Distances (the arc) were allowed to vary between trials but not within them. After a minimum delay of 15 minutes, the ape directed a caregiver to visible containers and, after each container was recovered, its contents were given to the subject. Visible and hidden trials (Experiment 2c, below) were conducted in alternating fashion in an approximately balanced order.

Results: Recovery order was significantly related to mean quantity in all four chimpanzees, and variance in three of four chimpanzees (Table 5, Fig. 3). All apes selected larger quantities before smaller ones, and all but Sherman selected variable containers before stable ones. For all subjects, the effect size for mean quantity was greater than that of variance. A significant interaction between mean quantity and variance was found only in Panzee, who distinguished between the mean quantity 16 containers far more sharply than she distinguished between the mean quantity 4 containers. Once again, as in Experiment 1b, chimpanzees utilized both quantity and variance associations when selecting visible containers. Also again, mean quantity exhibited a much larger effect with respect to container selection order than did variance; the effect size for variance was uniformly lower than when selections were made on an indoor tray (Experiment 1b). Interestingly, with containers visible and equidistant, Panzee utilized information she had learned indoors to guide her outdoor choices, unlike in Experiment 2a.

Experiment 2c - Containers hidden, distance controlled (20 trials/chimpanzee).—Experiment 2c was identical to 2b except that the containers were hidden; thus it was a memory problem.

Results: The mean quantity associated with containers was again significantly related to recovery order in all chimpanzees; variance was significantly related to recovery order in two of the four chimpanzees (Panzee and Sherman, Table 6, Fig. 4). Larger mean quantity containers were recovered earlier on average than smaller mean quantities; where significant differences existed, variable containers were taken on average earlier than stable ones. Again, effect sizes in all cases were greater for mean quantity than variance. There were significant interactions between mean quantity and variance for Mercury and Panzee, who again differentiated the mean 16 containers more sharply than the mean 4 containers.

Experiment 3: Risk preferences for a chicken nugget reward on an indoor testing tray—Experiment 3 was a dichotomous choice test, as in experiment 1a, but with

different containers and a different reward type. To highlight the variance factor, Experiment 3 involved only a single mean quantity of a rare and valuable food. All four chimpanzees were given experience with two unique containers with a distinctive mean quantity and variance of chicken nuggets. Again, the containers differed in shape and color but were approximately equivalent in volume. When present, chicken nuggets inside containers were sealed in a clear plastic bag; in situations where the variable negative reward applied, the container held an empty bag. The containers included: 1) stable 4 (a white cloth container measuring 14 cm height $\times$ 23 cm width $\times$ 15.5 cm depth), which always contained 4 chicken nuggets, and 2) variable 4 (a blue cloth container, 12.5 cm height $\times$ 22 cm width $\times$ 18 cm depth), which contained either 0 or 8 chicken nuggets with 0.5 probability of each.

Experience with containers: Individual chimpanzees were given 8 introductory sessions, during which each container appeared one time per session. This number of introductory sessions was chosen carefully—the goal was to allow the apes to learn the association between the containers and their set rewards/variances, while at the same time not satiating them on the “rare” food reward. Previous work with Lana and Sherman, and a rhesus monkey named Gale, has shown that all these primates can learn more difficult container-reward associations (5 colored eggs, each associated with a set quantity), with presumably less memorable food rewards (mini marshmallows), very quickly (essentially within a single 40 trial session, Beran et al. 2005).

Experimental sessions: Experimental sessions consisted of 20 dichotomous choice sessions of 1 trial apiece ($n = 20$ trials/chimpanzee). Both the stable 4 and variable 4 containers of chicken nuggets were presented simultaneously. The variable positive (8) and variable negative (0) quantities were presented an equal number of times across all sessions.

Results: Three of four chimpanzees showed risk aversion in that they significantly preferred the stable option with chicken nuggets as the reward. In contrast, only Lana significantly preferred the variable option (Table 7).

Experiment 4: Risk preferences for a chicken nugget reward in an outdoor testing area—The final experiment was a choice test designed to show whether the chimpanzees showed risk preferences as in Experiment 3, but in an outdoor, memory-based context. It involved a single mean and a constant distance; variance was again the only salient difference between container content.

Introductory outdoor choice trials and final experiment: In the introductory phase of the experiment, we gave each chimpanzee four trials in which they could choose between the stable 4 and variable 4 containers, both of which were visible. In the final experiment, we gave each chimpanzee 20 trials in which we hid the containers in pseudo-random locations equidistant from the subjects. After the chimpanzee chose one container and received its contents, we removed the other.

Results: The ratio of stable to variable selections in the introductory outdoor trials was 2:2 for Lana and 4:0 for Mercury, Panzee and Sherman. In the final experiment with containers

hidden, the chimpanzees showed no significant risk preferences, in contrast to those shown when the containers were on a tray and visible (Table 8).

Discussion

Four chimpanzees varied in their risk preferences when mean reward quantity, reward type, context, and experimental method were varied. Within and/or across subjects, outcomes differed when mean quantity changed from 4 to 16 peanuts, when rewards changed from peanuts to chicken nuggets, when tests were conducted outdoors instead of indoors, and when containers were hidden as opposed to being visible. A hypothetical ranking of our four chimpanzees on a 1–4 “risk-proneness” scale would vary substantially among experiments, and idiosyncratic differences were common. When tested in a classic indoor dichotomous choice procedure with peanuts (in containers) as the reward, individual apes were either risk-prone or risk-neutral, depending on mean quantity. These results are generally similar to those reported for chimpanzees in analogous tests (Heilbronner et al. 2008; Haun et al. 2011). In an indoor rank-ordering task involving four containers (two means, each with stable and risky options) all of the chimpanzees incorporated both mean quantity and variance information (again, in the direction of risk-proneness) in their selection order.

Any effects of variance, however, were easily disrupted. When the rank-ordering task was moved outdoors—where visible containers were more widely spaced, and intervals between observation and selection, and between trials, were increased—the effect sizes for mean quantity changed little, while those for variance decreased substantially.

The drop in effect size for the variance factor was even more striking in experiments where the containers were hidden from view, a fairly difficult memory problem involving retention of an indirect cue (containers representing possible food, as opposed to the food items themselves). Here, mean quantity was significantly related to recovery order almost universally, but relationships between variance and retrieval order were non-significant in all cases when “distance” varied, and idiosyncratically significant when distances were constant. It thus appears that at least some chimpanzees can retain information about both mean quantity and variance, and utilize such information in foraging decisions, even when the targets are outside of sensory range.

Just because a variable *can* be remembered and/or utilized in decision making, however, does not necessarily indicate that it is utilized in every situation. Previous work with two of the chimpanzees (Panzee and Sherman) has suggested that, when decisions are made concerning foods that were earlier observed being hidden, multiple variables can be incorporated into a single measure of “desirability” to generate efficient recovery orders. How these variables (e.g., quantity, average processing time, distance) are weighted appear to be related to their relative importance to the forager in question, and its individual abilities (e.g., abilities in pursuit and processing, Sayers and Menzel 2012). This illustrates well the adaptive nature of memory; an individual should remember those variables that are the most vital to remember. The low effect sizes of variance in the outdoor experiments suggests that this variable was given a rather low priority—a finding that could, of course, change in different contexts.

When the reward in a standard dichotomous choice was chicken nuggets, three of four chimpanzees exhibited risk-aversion. We consider two factors as being particularly relevant: 1) the rarity and preference value of the food type, and 2) the increased intervals between trials. Both of these considerations increase the severity of the gamble, and lengthened intertrial intervals have been associated with decreased risk-proneness in rhesus monkeys working a computer task (over a set of intertrial intervals admittedly shorter than in the present study, ranging from 1 to 90 seconds, Hayden and Platt 2007).

A necessary condition of the “rare food” variant was that prior exposure to the relevant containers was comparatively limited. Thus, another possible factor in our results is that one or more apes could not reliably estimate the outcome probabilities of the risky option—that the reward spectrum may have been, to some degree, ambiguous. Ambiguity aversion, indeed, has previously been reported for bonobos and chimpanzees (Rosati and Hare 2011). In addition, some theoretical treatments predict increasingly risk-averse behavior when parameter estimates of the variable option are uncertain (Kacelnik and Bateson 1996; McNamara 1996). Although relevant, we find an “incomplete information” interpretation unsatisfactory for the experiment in question. Unlike in Rosati and Hare (2011), where the apes possessed no information about reward possibilities in the “ambiguous” option, the present chimpanzees were under no such constraint. Moreover, they had learned more complex reward associations rapidly in previous studies (Rumbaugh and Washburn 2003; Beran et al. 2005; Menzel and Menzel 2012). In addition, the test objects contained particularly salient, memorable rewards, and the selections in the experimental trials were pointedly stable, involving little or none of the “sampling behavior” (i.e., picking the alternate container) expected when animals operate under the conditions of incomplete information (Stephens and Krebs 1986). Hiding the chicken nugget containers again reduced the variance effect, in this case to the point of risk-neutrality in all subjects.

These results, it is true, pertain to four individual chimpanzees, each with its own unique history, and in a limited number of experiments. Nevertheless, we maintain that there are broad cautionary lessons which can be drawn from them. As noted, merely changing quantity, food type, or spatial and temporal layout shifted the strength and/or direction of risk preferences for the apes in this study. Combined with previous work, this leads to a striking realization: there is little evidence to date that the variance preferences for any primate species (including, potentially, humans, March 1988), or larger taxonomic unit, are particularly robust across contexts or easily predictable. Indeed, in this experiment there were even notable differences between four individuals of a single species. It is premature to speak of risk-averse lemurs or bonobos, or risk-prone chimpanzees—as if risk preferences were well-characterized dimensions of temperament already known to be stable across situations—or to make strong claims about species contrasts.

This is not necessarily because genuine species-specific risk-sensitivity attributes do not exist, but rather because studies to date have been conducted in such a limited range of contexts (cf. Hurly and Oseen 1999; Bateson 2002). Results that hold over a computer screen may not hold over a tray, those over a tray may not hold in a field, and those in a field may not hold in the wild. Those that pertain to a species of fruit reward might not for another species of fruit, or a species of leaf.

In addition, unlike research with other vertebrates and invertebrates, ethical and practical considerations generally preclude serious reductions in primate food intake. In other words, the subjects are well-fed captive animals, and thus results must be interpreted with the provision that they apply to animals on neutral or positive energy balance—and, almost certainly, “more positive” than an average wild primate. As mentioned at the outset, risk-proneness is often expected to increase when animals are in negative energy balances (Caraco 1981).

Field data have been utilized to suggest that chimpanzees might act in the reverse direction—i.e., increased “risk-prone” hunting behavior when ripe fruit is more abundant and/or energetic status is likely more positive (Gilby and Wrangham 2007; Thompson et al. 2009; Watts and Mitani 2015). The present study offers considerations relevant to this discussion. For one, a meat reward, stripped of myriad factors that might influence hunting in a natural context (pursuit time and costs, less predictable success rates, group foraging, etc.) generally elicited contrasting risk profiles when compared to a peanut reward. This may reflect the relative value chimpanzees ascribe to meat that is easy to attain, somewhat analogous to an immature or exposed monkey in a free-ranging context. Perhaps more important, however, is that the number of contextual circumstances that influenced individual chimpanzee risk preferences would be expected to be greatly compounded in the wild; correlations between ripe fruit availability or energy balance and presumably “risky” behaviors such as hunting are unlikely to represent a complete story. The importance of variance to decision making may be secondary to other variables, may change depending on the precise animal or plant food categories involved, or may shift depending on individual or environmental context (such as the factors which might allow chimpanzees to gauge the likelihood of hunting success, Mitani et al. 2002). For this reason, field workers are especially encouraged to collect direct data on energetic (and other nutritional) returns, encounter rates, and variances for plant/animal prey species and types, as well as information on the sensory and memory capabilities involved in foraging decisions.

Primate risk studies have been conducted primarily by psychologists and anthropologists, and thus the focus has contrasted somewhat with that of researchers working with other organisms. Whereas ecologists generally have interpreted risk-sensitivity behavior as that of individuals who can shift their preferences (e.g., Caraco 1981), primate workers have more frequently looked to their subjects as providing information especially relevant to human neurophysiology (e.g., McCoy and Platt 2005), behavior, or evolution (e.g., Rosati and Hare 2011). All of these approaches are valuable, although studies aimed at phylogenetic reconstruction must come to terms with some special difficulties.

This is particularly the case when attempts are made to reconstruct character states of primate common ancestors, as Rosati and Hare (2011) attempted to do with regard to risk and ambiguity in the *Pan-Homo* clade. This involved the comparison of human studies with the results of tray testing in chimpanzees and bonobos and assuming that: 1) “ambiguity aversion” is a discrete, homologous trait, and 2) by parsimony or the “commonality principle” (Eldredge 1979; Latimer et al. 1981) it must have been present in the *Pan-Homo* last common ancestor. Although reconstructions such as this are a common practice in

primate cognition research, there are several limitations to them that are infrequently addressed.

One is that bonobos, chimpanzees, and humans represent only a scant sampling of the primates which make up the *Pan-Homo* clade, which includes numerous extinct hominids (*Ardipithecus*, *Australopithecus*, early *Homo*) known from the fossil record, and an unknown number of forms, in a parallel lineage, which predated chimpanzees and bonobos (Sayers and Lovejoy 2008; Sayers et al. 2012). The early hominid lineage is characterized by forms that differ from chimpanzees and bonobos in key features (e.g., habitat, dentition, locomotor anatomy), indicative of contrasting ecologies and social structures (Lovejoy 2009; Suwa et al. 2009). Reconstructions of common ancestors based only on living terminal taxa, when extinct forms within the group differ markedly across ecological contexts and geological time, must be made with caution.

A related concern is whether and to what degree “risk proneness,” “risk averseness,” or “ambiguity aversion” can be considered discrete biological characters—i.e., long-lasting, generalized dispositions of an organism to behave in particular ways (Mason 1986)—and whether the tests in question measure the same phenomena across taxa. Humans, for example, might evaluate their own uncertainty, or expected reward contingencies, differently than chimpanzees (Flavell 1979; Smith et al. 2012; Sayers et al. 2015), and relevant decision-making in ourselves might involve, at least in part, apomorphic neurophysiological pathways (Daw et al. 2006; Pasternak 2007). In such cases, assuming a discrete, unitary basis for the behaviors in question (the phenotypic gambit, Grafen 1984) must be tempered with an appreciation of their complexity and variation. Given the marked shifts in behavior that can be produced by subtle changes in context—as found with risk in the current study—it is doubtful that robust similarities within a species, let alone across taxa separated by millions of years, can be identified firmly by a brief period of study in any single experimental situation. It would require, at the least, a comparative consideration of the cross-situational consistency of the behavior, over different experimental paradigms (cf. Tinbergen 1963; Mason 1986).

In this study, as noted above, variance exerted less influence on individual chimpanzee decision making when the options were more widely spaced and/or hidden—i.e., in contexts that appear particularly relevant to natural primate foraging. Perhaps the apes were reacting to differences in the mean gains expected from the variable and stable containers based on subtle spatial or other factors (cf. Sayers and Menzel 2012), or utilizing variance information in extremely nuanced ways (e.g., as bees do, Harder and Real 1987; Real 1996). Perhaps the biggest question in risk-sensitivity research now is whether, and how, animals respond to variance in their natural habitats. For example, a primary importance of niche construction (e.g., insect fungiculture, human agriculture) might be that it reduces uncertainty, which implies that the effects of variation can be strong (Smith and Boyd 1990; Gremillion 1996; Dall 2010).

But with specific reference to foraging, surprisingly little work—beyond replications of classical lab procedures in a field setting—has attempted to evaluate the influence of risk in natural systems. When it has, the results have not always been easily interpretable: for

example, a risk-sensitivity explanation of web-site tenure in spiders (Gillespie and Caraco 1987) was later replaced with a simple social model based on conspecific interactions (Smallwood 1993), and a suggestive study implicating variance associations as a basis for bee dietary choices involved two target flower species that, while similar, may have differed subtly in their individual expected mean rates of return (Cartar 1991). Clearly, more work following these examples, as well as more experimental treatments in large-scale space, are necessary to tease apart the influence of the variables that help guide naturalistic feeding behavior. Part of the challenge is to incorporate factors beyond food intake, such as likelihood of predator or competitor presence, with how variance is estimated (e.g., the effects of extragroup depletion on baboon patch choice, Noser and Byrne 2010)

Studies in risk-sensitivity, as noted, have often been couched as challenges to “deterministic” optimal foraging theory (Kacelnik and Bateson 1996). This is certainly correct in the sense that treatments such as the classical optimal diet model do not concern themselves with variance (Stephens and Krebs 1986). But, surprisingly, these models often do quite well in predicting animal behavior in both laboratory and field, and over a diverse range of situations and taxa (Sih and Christensen 2001). The most reasonable interpretation is that, whereas they do not include every relevant variable, they include crucial ones, with robust predictive value. Models, after all, are generalized abstractions (Rosenbluth and Wiener 1945; Sayers 2015), and researchers often prefer utilizing the simplest one necessary for the task at hand. So it goes with classical optimal foraging theory; there are situations where, undoubtedly, these simple treatments perform as well or better than more complex models that include variance as a factor.

Life is indeed uncertain, and keeping the dessert fork closest to the plate is a sensible idea. But as for the functional reasons for such behavior, dessert might differ from the main course in a multitude of ways; it might be sweeter, more energy-packed, prepared by a different chef, closer, scarcer, easier to swallow, or more predictable. With respect to animal foraging behavior, it is no longer adequate to document mere sensitivity to variance. It is time to determine how much of the “variance,” so to speak, that variance actually explains.

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Significance statement

Studies of risk sensitive foraging traditionally include two options (of differing variances) that involve the same food type, are close to one another, and are visible to the decision maker. We examined risk sensitivity in four chimpanzees, and included experiments that involved four options, differing food rewards, increased distance between options, and/or choosing between items visually hidden at the time of decision making. We found that chimpanzees exhibited sensitivity to variance, and could utilize mean quantity and variance associations—even in some cases when the items were not visible. However, differences within or between individual apes in the strength or direction of risk preferences occurred when experimental context (e.g., reward type, visible/hidden) was varied. These results suggest that identifications of primate species-specific risk preferences are premature, and that studies of risk should be conducted in a wider range of contexts.

Fig. 1.

Experiment 1b: 95% confidence interval for mean selection order of containers in a 1-2-3-4 rank ordering task on indoor testing tray, peanut reward, for each individual chimpanzee. V = variable, S = stable. Number denotes mean quantity

Fig. 2.

Experiment 2a: 95% confidence interval for mean selection order of containers in a 1-2-3-4 rank ordering task with containers hidden in outdoor test area, peanut reward, for each individual chimpanzee; distance from subject to individual containers free to vary. Notation as in Fig. 1

Fig. 3.

Experiment 2b: 95% confidence interval for mean selection order of containers in a 1-2-3-4 rank ordering task with visible containers placed in outdoor test area, peanut reward, for each individual chimpanzee; distance from subject to individual containers controlled. Notation as in Fig. 1

Fig. 4. Experiment 2c: 95% confidence interval for mean selection order of containers in a 1-2-3-4 rank ordering task with containers hidden in outdoor test area, peanut reward, for each individual chimpanzee; distance from subject to individual containers controlled. Notation as in Fig. 1

Table 1

Studies of risk in nonhuman primates, with classical procedures

Taxon or Taxa	Spatial scale & reward	Results	Notes	Citation(s)
Ring-tailed lemur (<i>Lemur catta</i>) Mongoose lemur (<i>Eulemur mongoz</i>) Red ruffed lemur (<i>Varecia rubra</i>)	Computer screen; food pellets	Risk-averse; preferred stable option even when mean reward of variable option was 2x greater	Authors associate result with behavior tendencies that evolved to cope with unpredictable Malagasy island habitats	MacLean et al. 2012
Rhesus macaque (<i>Macaca mulatta</i>)	Testing tray (WGTA); popcorn kernels	Risk-averse or risk-neutral	Experimentally-experienced monkeys "avoided nonreward" (were risk-averse); naïve monkeys were risk neutral	Behar 1961
Rhesus macaque (<i>Macaca mulatta</i>)	Computer screen; liquid reward	Risk-prone	Increased neuronal activity in posterior cingulate cortex scales positively with degrees of risk	McCoy and Platt 2005
Rhesus macaque (<i>Macaca mulatta</i>)	Computer screen; liquid reward	Risk-prone or risk-neutral	Risk-prone behavior declines to neutrality with increasing interval between trials	Hayden and Platt 2007
Rhesus macaque (<i>Macaca mulatta</i>)	Computer screen; liquid reward	Risk prone	Monkeys preferred "gambles" to stable option, and also to an alternating option	Hayden et al. 2008
Orangutan (<i>Pongo pygmaeus</i>) Gorilla (<i>Gorilla gorilla</i>) Bonobo (<i>Pan paniscus</i>) Chimpanzee (<i>Pan troglodytes</i>)	Testing tray; varying sizes of two banana slices shown to apes then hidden, with larger reward always placed covertly under 1 to 4 "risky" cups	All risk-prone	As size of safe option increases, animals become less risk-prone; orangutans and chimpanzees more risk-prone than gorillas or bonobos	Haun et al. 2011
Bonobo (<i>Pan paniscus</i>) Chimpanzee (<i>Pan troglodytes</i>)	Testing tray; grapes	Bonobos risk-averse; Chimpanzees risk-prone	Authors attribute results to "riskier" foraging ecology of chimpanzees relative to bonobos	Heilbronner et al. 2008

Table 2

Results of Experiment 1a: proportion of stable container selections in dichotomous choice task on indoor testing tray, peanut reward

	mean = 4			mean = 16		
	stable choices	p-value	risk-	stable choices	p-value	risk-
Lana	0.19	< 0.001*	prone	0.17	< 0.001*	prone
Mercury	0.24	< 0.001*	prone	0.08	< 0.001*	prone
Panzee	0.53	0.62	neutral	0.18	< 0.001*	prone
Sherman	0.48	0.76	neutral	0.25	< 0.001*	prone

Stable choices given as proportion of all trials (n = 100/mean quantity/chimpanzee). An asterisk (*) denotes a significant result

Table 3

Results of experiment 1b: effect sizes of fixed factors mean quantity and variance to selection order in a 1-2-3-4 rank ordering task on indoor testing tray, peanut reward

	Adjusted R Squared	Mean order selected	Mean Quantity F p Partial Eta Squared	Variance F p Partial Eta Squared	Interaction: MQ * V F p Partial Eta Squared
Lana	0.90	V16, S16, V4, S4	1371.01 < 0.001* 0.88	266.47 < 0.001* 0.59	0.63 0.43, NS 0.003
Mercury	0.85	V16, S16, V4, S4	849.00 < 0.001* 0.82	189.07 < 0.001* 0.50	8.68 0.004* 0.04
Panzee	0.69	V16, S16, S4, V4	328.49 < 0.001* 0.64	39.36 < 0.001* 0.17	66.14 < 0.001* 0.26
Sherman	0.82	V16, S16, V4, S4	759.43 < 0.001* 0.80	82.54 < 0.001* 0.31	26.50 < 0.001* 0.12

Results are from a General Linear Model ANOVA with order selected as dependent variable and mean quantity and variance as fixed factors (model, df = 3; fixed factors and interaction, df = 1). F = F statistic, p = probability, MQ = mean quantity, V = variance, NS = not significant. An asterisk (*) denotes a significant result

Table 4

Results of Experiment 2a: effect sizes of fixed factors mean quantity and variance to selection order in a 1-2-3-4 rank ordering task with containers hidden in outdoor test area, peanut reward; distance from subject to individual containers free to vary

	Adjusted R Squared	Mean order selected	Mean Quantity F p Partial Eta Squared	Variance F p Partial Eta Squared	Interaction: MQ * V F p Partial Eta Squared
Mercury	0.37	V16, S16, S4, V4	45.69 < 0.001* 0.38	0.39 0.53, NS 0.01	2.65 0.11, NS 0.03
Panzee	0.04	V16/S4, S16/V4	0.00 1.00, NS 0.00	0.00 1.00, NS 0.00	5.90 0.02* 0.07
Sherman	0.65	V16, S16, V4, S4	145.27 < 0.001* 0.66	2.80 0.10, NS 0.04	0.11 0.74, NS 0.001

Involves recovery of hidden items, outdoors, after a minimum 15 minute delay. Results are from a General Linear Model ANOVA with order selected as dependent variable and mean quantity and variance as fixed factors (model, df = 3; fixed factors and interaction, df = 1). F = F statistic, p = probability, MQ = mean quantity, V = variance, NS = not significant. An asterisk (*) denotes a significant result. A "slashed" result (e.g., V16/S4) denotes equivalence

Table 5

Results of Experiment 2b: effect sizes of fixed factors mean quantity and variance to selection order in a 1-2-3-4 rank ordering task with visible containers placed in outdoor test area, peanut reward; distance from subject to individual containers controlled

	Adjusted R Squared	Mean order selected	Mean Quantity F p Partial Eta Squared	Variance F p Partial Eta Squared	Interaction: MQ * V F p Partial Eta Squared
Lana	0.80	V16, S16, V4, S4	293.39 < 0.001* 0.79	15.62 < 0.001* 0.17	0.77 0.38, NS 0.01
Mercury	0.82	V16, S16, V4, S4	355.56 < 0.001* 0.82	10.89 0.001* 0.13	2.00 0.16, NS 0.03
Panzee	0.54	V16, S16, V4, S4	71.49 < 0.001* 0.49	12.24 0.001* 0.14	10.29 0.002* 0.12
Sherman	0.76	V16, S16, V4, S4	248.06 < 0.001* 0.77	1.47 0.23, NS 0.02	0.65 0.42, NS 0.01

Involves recovery of visible items, outdoors, after a minimum 15 minute delay. Results are from a General Linear Model ANOVA with order selected as dependent variable and mean quantity and variance as fixed factors (model, df = 3; fixed factors and interaction, df = 1). F = F statistic, p = probability, MQ = mean quantity, V = variance, NS = not significant. An asterisk (*) denotes a significant result

Table 6

Results of Experiment 2c: effect sizes of fixed factors mean quantity and variance to selection order in a 1-2-3-4 rank ordering task with containers hidden in outdoor test area, peanut reward; distance from subject to individual containers controlled

	Adjusted R Squared	Mean order selected	Mean Quantity F p Partial Eta Squared	Variance F p Partial Eta Squared	Interaction: MQ * V F p Partial Eta Squared
Lana	0.21	V16, S16, S4, V4	17.98 < 0.001* 0.19	2.44 0.12, NS 0.03	3.19 0.08, NS 0.04
Mercury	0.68	V16, S16, S4, V4	160.42 < 0.001* 0.68	1.11 0.30, NS 0.01	10.03 0.002* 0.12
Panzee	0.38	V16, S4, S16, V4	12.48 0.001* 0.14	10.76 0.002* 0.12	28.07 < 0.001* 0.27
Sherman	0.65	V16, S16, V4, S4	138.13 < 0.001* 0.65	11.28 0.001* 0.13	0.11 0.74, NS 0.001

Involves recovery of hidden items, outdoors, after a minimum 15 minute delay. Results are from a General Linear Model ANOVA with order selected as dependent variable and mean quantity and variance as fixed factors (model, df = 3; fixed factors and interaction, df = 1). F = F statistic, p = probability, MQ = mean quantity, V = variance, NS = not significant. An asterisk (*) denotes a significant result

Table 7

Results of Experiment 3: proportion of stable container selections in dichotomous choice task on indoor testing tray, chicken nugget reward

	Stable choices	p-value	risk-
Lana	0.25	0.04*	prone
Mercury	0.95	< 0.001*	averse
Panzee	1.00	< 0.001*	averse
Sherman	1.00	< 0.001*	averse

Test performed indoors on a sliding tray. Stable choices given as proportion of all trials (n = 20). An asterisk (*) denotes a significant result

Table 8

Results of Experiment 4: proportion of stable selections in dichotomous choice task with containers hidden in outdoor test area, chicken nugget reward; distance from subject to individual containers controlled

	Stable choices	p-value	risk-
Lana	0.40	0.50	neutral
Mercury	0.50	1.00	neutral
Panzee	0.55	0.82	neutral
Sherman	0.50	1.00	neutral

Containers hidden in an outdoor testing area with a minimum 15 minute delay before recovery. Stable choices given as proportion of all trials (n = 20) where the chimpanzee first directed a naïve human searcher to the location of that container