The Power of Nothing:

Risk Preference in Pigeons, But Not People,

Is Driven Primarily by Avoidance of Zero Outcomes

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Abstract

Both human and non-human animals regularly need to make choices where the outcomes of their actions are unpredictable or probabilistic in some way. These are often termed "risky" choices. Faced with uncertain rewards, people (*Homo sapiens*) and pigeons (*Columba livia*) often show similar choice patterns. When the reward probabilities of risky choices are learned through experience, preferences in both species seem to be disproportionately influenced by the extreme (highest and lowest) outcomes in the decision context. Overweighting of these extremes increases preference for risky alternatives that lead to the highest outcome and decreases preference for risky alternatives that lead to the lowest outcome. In a series of studies, we systematically examine how this overweighting of extreme outcomes in risky choice generalizes across two evolutionary distant species: pigeons and humans. Both species showed risky choices consistent with an overweighting of extreme outcomes when the low-value risky option could yield an outcome of zero. When all outcome values were increased such that none of the options could lead to zero, people but not pigeons still overweighted the extremes. Unlike people, pigeons no longer avoided a low-value risky option when it yielded a non-zero food outcome. These results suggest that, despite some similarities, different mechanisms underlie risky choice in pigeons and people.

Keywords: risky choice; decisions from experience; comparative cognition; decision making

When confronted with uncertain rewards, humans and other animals often show similar preferences for varying levels of risk (e.g., Lagorio & Hackenberg, 2013; Ludvig et al., 2014; Weber et al., 2004). Humans generally tend to be risk averse for gains (e.g., Kahneman & Tversky, 1979), while other animals are often risk averse for reward amount, but risk seeking for reward delays (e.g., Kacelnik & Bateson, 1995; Mazur, 1984, 1986). These risk preferences, however, can vary with context depending on how the potential outcomes are encountered (e.g., Hertwig & Erev, 2009; Madan, Ludvig, & Spetch, 2019) or the range of other outcomes that are available (e.g., Ludvig et al., 2014a; Stewart, 2009). For example, one recent study compared risky choice in pigeons and humans, finding that risk preferences in both species was influenced by an oversensitivity to the extreme outcomes, highest and lowest, encountered (Ludvig et al., 2014b). In this paper, we build on that result, by assessing risky choice with a broader range of possible outcomes, systematically assessing to what degree the risk preferences of pigeons and humans reflect common underlying psychological processes.

In non-human animals, a wide range of risk preferences for rewards have been documented: many studies have shown risk aversion as in humans (e.g., Bateson & Kacelnik, 1995), but some have found risk neutrality or even risk seeking (e.g., Barnard, Brown, Houston, & McNamara, 1985; Hayden, Heilbronner, Nair, & Platt, 2008). Even within a single species, such as pigeons, behavioural effects can vary across experiments (Lagorio & Hackenberg, 2012). Moreover, risk preferences may depend on factors such as energy budget (Caraco, Martindale, & Whittam, 1980; Stephens, 1981), choice framing (e.g., Constantinople, Piet, & Brody, 2018; Lakshminarayan, Chen, & Santos, 2011; Marsh & Kacelnik, 2002), and the recent outcomes of a choice (Marshall & Kirkpatrick, 2013).

In humans, risky choice is typically assessed using scenarios in which the probabilities and outcomes are explicitly described. When people learn about the consequences of their risky choices through experience, however, different choice patterns often emerge—a discrepancy referred to as the *description-experience gap* (e.g., Barron and Erev, 2003; Camilleri & Newell, 2011; Hertwig & Erev, 2009, Ludvig & Spetch, 2011; Ungemach, Chater, & Stewart, 2009). For example, with described choices, people tend to be more risk seeking when the choice is between two types of losses than two types of gains (e.g., Kahneman & Tversky, 1979). In contrast, when outcomes are learned through experience, people sometimes reverse these preferences and are more risk seeking for gains than for losses (Ludvig & Spetch, 2011; Madan, Ludvig, & Spetch, 2017; Tsetsos et al., 2012). Learning from experience is also more similar to how non-human animals make decisions (but see Constantinople, Piet, & Brody, 2018; Heilbronner & Hayden, 2016).

One explanation for the pattern of risk preferences in experience-based choice is that the most extreme values encountered in a decision context are overweighted (e.g., Ludvig, Madan, & Spetch, 2014a; Ludvig et al., 2018). For example, consider a context where there are 4 possible options: a safe gain of +20 points, a risky 50/50 chance of +40 or 0 points, a safe loss of −20 points, and a risky 50/50 chance of −40 or 0 points. In this context, the best possible outcome is +40 and the worst possible outcome is −40. Overweighting of these extremes would thus produce more risk seeking in choices between the gains (where the extreme is good) and risk aversion in choices between the losses (where the extreme is bad). People do indeed overweight the extremes when repeatedly choosing between options that led to safe and risky gains and losses (Ludvig, & Spetch, 2011; Ludvig et al., 2014a; Madan et al., 2014).

In a previous cross-species comparison, we found evidence suggesting that pigeons also

overweight the extreme outcomes (Ludvig, Madan, Pisklak, & Spetch, 2014b). Pigeons were

tested in a foraging analogue of the human decision-making task in which they chose by walking

behind one of two distinct panels to obtain food rewards (see Figure 3). As in the human task

above, there were four possible options: Two of the panels provided high-value outcomes: one

panel led to a 50/50 chance of 2 or 4 food rewards and the other panel always led to 3 food

rewards. The two other panels provided low-value outcomes: one panel led to a 50/50 chance of

0 or 2 food rewards, and the other panel always led to 1 food reward. The pigeons' choices were

compared to those of humans who participated in a computer-based task with doors that similarly

led to risky or safe numbers of points exchangeable for money. Both species were more risk

seeking for high-value gains than for low-value gains, as though they were overweighting the

extreme outcomes.

Humans consistently overweight extremes across many different sets of outcome values

(see Madan et al., 2019, for a review). Pigeons, however, have only been tested with a single set

of outcome values (0 to 4; Ludvig et al., 2014b). Whether the overweighting of extremes would

generalize to other values for pigeons is not known. One alternative possibility is that the

seeming overweighting of extremes by pigeons was actually due in part, or even largely, to an

avoidance of zero outcomes. Although the pigeons showed risk seeking for high-value choices

and risk aversion for low-value choices, the deviation from indifference for the low-value

choices was more pronounced (Ludvig et al., 2014). Moreover, in their procedure, a zero

outcome represented the absence of food reward, which meant that selection of the low-value

risky option was only intermittently reinforced, whereas the low-value safe option was

continuously reinforced, albeit at a smaller reinforcer magnitude.

With humans, the possibility that an aversion to zero outcomes is responsible for the risk

preferences was ruled out by eliminating zero outcomes and still observing the same

overweighting of extremes (e.g., Ludvig et al., 2014a). With pigeons, however, the contribution

of zero outcomes to the extreme-outcome effect has not yet been evaluated. Indeed, animals

likely process the concept of zero differently from humans (Nieder, 2016). The present

experiments were thus designed to more extensively evaluate the correspondence between

pigeon and human risky choice observed by Ludvig et al. (2014b) and to test whether the similar

patterns of choice were produced by the same psychological mechanism. Experiment 1 was a

conceptual replication of their risky-choice task using an operant task that was more similar

across species. Experiment 2a tested risk preferences in the absence of zero values using an

open-field task in pigeons (as in Ludvig et al., 2014b) and with the same operant task in people.

Experiment 3 directly manipulated the occurrence of zero with the operant task with pigeons.

Lastly, Experiment 4 examined pigeons' risk preferences without zero outcomes after an

evaluation of their capacity to discriminate between the different reward magnitudes.

Experiment 1: Zero Outcomes

The first experiment developed a new operant task for comparing risky choice across

pigeons and humans (see Figure 1). In the task, both species selected between pairs of coloured

circles that represented risky and safe outcomes of high or low value, ranging from 0 to 4 (as

above; see Ludvig et al., 2014b). Pigeons were reinforced with food and humans with points that

were exchanged for money. If extremes are overweighted, then both pigeons and humans should

select the risky option significantly more often when choosing between risky and safe high-value options than between risky and safe low-value options. Avoidance of zero values should also produce a difference in risk preference, driven by strong risk aversion for the low-value choices.

Experiment 1a: Pigeons

Subjects. Six adult pigeons (*Columba livia*) — four Racing Pigeons and two Silver King — selected from a University of Alberta pigeon colony were used. All pigeons had extensive learning histories, but none had served in studies of risky choice. They were individually housed in a temperature-controlled colony with a 12-hour light-dark cycle. Free access to grit and vitamin-enriched water was provided, and each pigeon was maintained at approximately 85% of its free-feeding weight by food pellets obtained during and after experimental sessions. All procedures were approved by the University of Alberta Biological Sciences Animal Care and Use Committee, following the guidelines of the Canadian Council on Animal Care. All pigeons passed the exclusion criterion and were included in the analyses (see Data Analysis section).

Apparatus. A custom-built 71.1 × 33.0 × 44.5 cm sound-attenuating operant-conditioning chamber, located in an isolated room, was used. A 17-in. ViewSonic LCD monitor was mounted centrally against the chamber's widest wall, equipped with a Carrol Touch infrared touchscreen (Elo Touch Systems Inc., Menlo Park, CA). Two feeding ports, adjacent to both sides of the monitor, provided access to food pellets via a solenoid-controlled food hopper containing Mazuri food pellets. A light within each feeding port signalled when the hopper had been raised, and an infrared beam detected entry into the port. Each chamber was connected to a computer in an adjacent room. E-Prime 2.0 software (Psychology Software Tools, Pittsburgh, PA) was used to control contingencies and detect responses.

Stimuli. Experimental stimuli consisted of coloured circles (white, black, purple, green, yellow, and orange) presented against a grey background on the monitor. Each circle had a diameter of 100 pixels (approximately 2.5 cm).

Procedure. Sessions lasted for 45 min and were run six days a week at approximately the same time each day.

Training Phase 1. This phase entailed an autoshaping procedure that presented white circles either centrally on the screen or to the right or left of centre, or black circles in numerous spatial locations. Trials began with a single white or black circle (each with a 50% chance). The circle remained onscreen for 60 s or until it was pecked. It then disappeared and a randomly-selected hopper was raised allowing the pigeon 1 s of food access. Access was timed from the initial moment the pigeons head entered the feeding port. This was followed by a 20-s inter-trial interval (ITI). The spatial location of each presented circle was selected randomly without replacement from a list of locations. Autoshaping continued until the pigeons responded on more than 75% of the total stimulus presentations. Phase 1 lasted for a mean of 2.17 and range of 1-3 sessions.

Training Phase 2. This phase entailed an operant procedure in which the ITI was shortened to 2 s and a peck at the circle was required to raise a hopper. This phase continued until the pigeons completed 50 trials within a 45-min session, requiring a mean of 1.33 and range of 1-3 sessions.

Training Phase 3. In this phase, sessions consisted of only 16 trials, and the stimuli appeared in a sequence that resembled the testing procedure. First, a white circle (start stimulus) appeared centrally on the screen. A single peck at the start stimulus erased it and produced

another white circle on the left or right. Pecking the new circle erased it and produced 1, 2, 3, or

4 black circles (tokens) according to the layouts depicted in Figure 1. A single peck at each token

produced 1-s access to food. Once all tokens had been selected, a 2-s ITI ensued. Pigeons

remained on this phase until their weight stabilized to approximately 85% of their free-feeding

value, which required a mean of 13.5 and range of 10-15 sessions.

  Training Phase 4. This phase consisted of four sessions, each containing 16 single-

option trials with yellow, green, orange, and purple circles. This phase provided forced exposure

to the stimuli and reward contingencies that would occur in testing, with the order and side

presentation randomized across trials.

  Testing. Testing consisted of 80 sessions, each lasting up to 60 minutes with 16 trials.

Figure 1 shows a schematic of an example trial. Each trial began with the centrally-presented

white start-stimulus. A single peck to this stimulus caused it to disappear and one or two

coloured (choice) circles appeared on either side. A single peck to a choice circle erased it and

produced 0, 1, 2, 3, or 4 black circles (tokens) as shown in Figure 1. There were four choice

options. The *risky-high* option led to 2 or 4 tokens each with a 50% chance. The *risky-low* option

led to 0 or 2 tokens each with a 50% chance. The *safe-high* option always led to 3 tokens, and the

safe-low option always led to one token. A single peck to any of the tokens caused it to disappear

and a randomly-selected food hopper to rise, providing 1-s of food access. The bird could then

select any remaining token for another 1-s of food access until all tokens were removed. After a

2-s ITI, a new trial began.

  Each session included three trial types: *Risk-preference* trials presented a choice between

a risky-high and a safe-high option, or a risky-low and a safe-low option. *Catch* trials presented a

choice between a high and low reward option, with all four possible choice combinations. For instance, given a choice between a risky-high and safe-low alternative (see Figure 1), the former provides 3 rewards *on average* and the latter only provides 1. Given that one of the catch alternatives always contains a higher average reward payout (more food reinforcement), that alternative is expected to be preferred. Because catch trials facilitate these obvious preferences, they were used as a means of assessing how well the task's contingencies are learned. *Single-option* trials presented only one option that had to be selected, ensuring that all options were occasionally chosen and all outcome contingencies were experienced. Each session included four risk-preference trials (two high and two low), eight catch trials and four single-option trials, with trial order randomized within the session and counterbalanced such that each choice stimulus appeared equally often on the left or right. All possible combinations of stimuli and reward outcomes were counterbalanced across every four sessions.

Experiment 1b: Humans

Participants. Thirty participants (aged [$M\pm SD$] 20.5 ± 2.1 years old; 20 females) recruited from the University of Alberta undergraduate psychology participant pool participated for course credit. All participants provided informed consent, and procedures were approved by the University of Alberta research ethics board. Seven participants were excluded from the analysis due to failure to pass the catch trial criterion.

Procedure. Participants first sat as a group, and instructions were simultaneously read aloud and projected on a screen (see Appendix A). Participants then entered individual rooms to complete the computer task using a mouse to make choices. Visually, the task was identical to the pigeon testing procedure, except that a cumulative point tally was displayed at the bottom of

the screen. Each click on a token raised this tally by 1 point. The experimental session was

divided into 8 blocks of 64 trials. To provide a break, participants performed a maze task

between blocks. The first block provided 64 single-option trials. All subsequent blocks provided

16 risk-preference trials, 32 catch trials, and 16 single-option trials. Trial types were randomly

intermixed and provided every possible combination of choice stimulus, side, and reward.

After the experiment, participants' cumulative points were converted to a cash bonus of

up to $5.00. Participants were not told the conversion rate prior to the experiment. The

conversion was based on a linear increase from the fewest possible points (744 points = $0.00),

through the points expected by chance (1024 points = $2.50), to the maximum possible points

(1304 points = $5.00).

Data Analysis

For consistency with prior work (Ludvig et al., 2014b), the final third of the total

collected choices were used for statistical analysis, which was conducted using R Software for

statistical computing (R Core Team, 2018). As in prior studies (e.g., Ludvig & Spetch, 2011;

Ludvig et al., 2014b), pigeons or humans who showed less than 60% accuracy in choosing the

high-value option across all catch-trial types were excluded from analyses. The rationale is that if

subjects do not reliably choose more reward (points/money or food) over less reward, then they

either did not adequately learn the reward contingencies or were not motivated by the potential

rewards, making their risk preference results difficult to interpret.

For risk-preference trials, a paired t-test was conducted on the proportion of risky option

selections for the high- and low-value choice types. For catch trials, a paired t-test was conducted

on the proportion of high-value option selections across trials with and without the lowest-

extreme (i.e., 0) as a possible outcome. Additionally, a JZS Bayes factor (BF_{10}) with a medium

prior was computed for each comparison to obtain the relative odds in favor of the alternative

hypothesis over the null using the BayesFactor R package (Morey & Rouder, 2011, 2018). Effect

sizes of mean differences used an unbiased estimate of Cohen's *d* (i.e., Hedges' *g*), and 95%

confidence intervals were computed using the effsize package (Torchiano, 2017).

Results

Figure 2A (pigeons) and Figure 2B (humans) show the mean proportion of risky option

selections for high-value and low-value choices, and the paired differences between these choice

types with 95% confidence intervals (Franz & Loftus, 2012). For high-value choices, risky

option selection refers to choosing the stimulus leading to either 2 or 4 instead of the stimulus

leading to a guaranteed 3. For low-value choices, risky option selection refers to choosing the

stimulus leading to 0 or 2 instead of the stimulus leading to a guaranteed 1. On average, pigeons

chose the risky option significantly more often for high-value (M = .58, 95% CI [0.45, 0.72])

than for low-value choices (M = .10 [−0.02, 0.22]), $t(5)$ = 11.45, p < .001, g = 4.31 [1.97, 6.67],

BF_{10} > 150. Similarly, humans reliably selected the risky option more for high-value (M = .57

[0.43, 0.71]) than low-value choices (M = .29 [0.18, 0.41]), $t(22)$ = 5.09, p < .001, g = 1.04 [0.41,

1.68], BF_{10} > 150.

Figure 2 depicts aggregated learning curves for pigeons and humans on catch trials.

Pigeons chose the high-value option more often when the low-value option sometime led to the

lowest extreme (i.e., the option leading to 0 or 2) than when that lowest extreme was not possible

(i.e., the option always leading to 1). Thus, catch trials containing an option that sometimes

provided no food reward were learned the most readily. For pigeons, this difference between the

two types of catch trials was significant; $t(5) = 4.35$, $p = .007$, $g = 1.64$ [0.15, 3.13], $BF_{10} = 8.7$.

The human catch-trial data revealed no such differentiation, as near-ceiling effects were

observed across all types of catch trials; $t(22) = 1.16$, $p = .257$, $g = 0.24$ [–0.36, 0.84], $BF_{10} = 0.4$.

Discussion

In this novel operant task, pigeons and humans exhibited similar levels and patterns of

risk preference. Both species selected the risky option more often for high-value than for low-

value choices, as though they were overweighting the extreme outcomes (Ludvig et al., 2014a).

The possibility of receiving 4 rewards seemed to pull preference towards the risky high-value

option, whereas the possibility of receiving 0 rewards pushed preference away from the risky

low-value option. These results replicate and extend the core findings of Ludvig et al. (2014b) to

a novel experimental domain.

The catch-trial performance, however, suggests that pigeons' choices might have been

driven more strongly by an avoidance of the zero reward than humans. This observation raises

the possibility that the risk aversion exhibited by pigeons on low-value trials may have been

driven at least in part by an explicit avoidance of a zero reward (also in Ludvig et al., 2014b).

Humans did not show the same asymmetry in their catch-trial performance, and other

experiments with humans have shown that eliminating the zero, or no-reward outcomes, does not

qualitatively change the results (Ludvig et al., 2014a). Thus, humans may be more sensitive to

any extreme outcomes, whereas pigeons may be more sensitive to zero outcomes. Experiment 2

tested this possibility.

Experiment 2: Non-Zero Outcomes

This experiment tested risk preferences for high- and low-value rewards, but with each value increased by one to make the lowest possible value a non-zero outcome. The experimental design was similar to Experiment 1, but the task for pigeons differed. Because catch-trial performance of Experiment 1 and initial pilot data suggested that pigeons had difficulty learning the necessary discriminations with all non-zero values in an operant procedure, the foraging procedure described in Ludvig et al. (2014b) was used. Humans were tested with the same operant procedure as in Experiment 1.

Experiment 2a: Pigeons

Subjects. Six pigeons (*Columba livia*) (three Racers and three Silver King), all with substantial learning histories, but no experience in risky-choice experiments were housed and maintained as in Experiment 1. Each pigeon was run daily, five days a week, at the same time each day.

Apparatus. Figure 3 shows a photo of the experimental arena. The arena consisted of two compartments separated by a 50.8-cm central wall and enclosed by 91.4-cm front and rear walls and a single 82.5-cm side wall. The central and rear walls were built of 1.27-cm thick plywood painted white. The front and side walls were made from thin, white corrugated plastic. The arena floor was layered with aspen-chip bedding.

Two 44.45 × 63.50 cm white corrugated plastic entry doors, each at a 45° angle from the central wall, formed a small, triangular *decision area* at the front of the arena. Doors opened via a pulley system. A 16.51 × 20.32 cm entrance in the wall of the decision area led to a plastic 48.26 × 39.37 × 101.60 cm start box. Pigeon behaviour was monitored and recorded by a closed-circuit camera mounted centrally on the ceiling.

Stimuli. Choice panels consisted of two 30.48 × 58.42 cm planks of 2.54 cm thick plywood set at a 90° angle and covered with laminated paper of distinct colours (green, orange, purple, and yellow) and designs (a hollow black triangle, three horizontal black lines, four white squares, and a black "X"; see Figure 3 for an example). Two additional solid white training panels were used in Phase 2. The panels were centered inside the compartments, and food rewards were concealed behind each choice panel. Each individual food reward consisted of two Mazuri Gamebird pellets placed on top of grit inside a 6.99-cm diameter ceramic cup.

Procedure. Preliminary training occurred over several days in three phases:

Training Phase 1. Pigeons were trained via successively reinforced approximations to enter each compartment from the start-box through either entry door (randomly chosen), walk to the furthest corner to obtain three food rewards, and then return to the start box. This lasted for a mean of 4.33 and range of 2-8 sessions.

Training Phase 2. A white choice panel was placed in the centre of each compartment and pigeons were gradually shaped to walk around the panel to obtain food and return to the start-box. Phase 3 began once pigeons reliably completed 16 trials within a session, with all food rewards concealed behind the panel. This lasted for a mean of 4.83 and range of 2-8 sessions.

Training Phase 3. Pigeons completed 64 single-option trials randomly distributed over four 16-trial sessions. To start a trial, the door to one of the compartments opened, and the barrier into the decision area from the start-box was removed. Once the pigeon entered a compartment, the door was closed to prevent re-entry into the decision area until all food rewards were consumed. The door was then re-opened allowing the pigeon to return to the start-box, which now contained a food cup with 2 pellets.

The four panels indicated a *risky* or *safe* outcome of either *high* or *low value*. The safe high-value panel always indicated 4 rewards, and the risky high-value panel indicated a 50/50 chance of 3 or 5 rewards. The safe low-value panel always indicated 2 rewards, while the risky low-value panel indicated a 50/50 chance of 1 or 3 rewards. Panel presentation was counter-balanced and randomized across the 64 trials such that each panel and reward occurred equally often on each side.

Testing. Testing lasted for 28 sessions that each contained four single-option trials, which exposed the bird once to each of the four panels, and 12 choice trials, which consisted of four *risk-preference trials* and eight *catch trials*. On risk-preference trials, pigeons chose between safe and risky options of the same expected value (e.g., risky high-value vs. safe high-value). Catch trials provide a choice between one high-value (risky or safe) and one low-value panel (risky or safe). Each session had two of each type of catch trial. Sessions were counterbalanced so that each stimulus appeared twice in both the right and left compartments on choice trials. Ordering of the trials was randomized each session.

The testing procedure was identical to Phase 3 except that both entry doors opened simultaneously on each trial. On single-option trials, one of the compartments was left empty. If the pigeon entered the empty side, both guillotine doors were left open until the pigeon entered the side with a panel.

Experiment 2b: Humans

Participants and Methods.

Group 1: Forty-four participants (aged 20.3 ± 2.3 years old; 35 females) were recruited from the same participant pool as Experiment 1b; no individuals participated in more than one

experiment. In this experiment, the risky high-value option produced 3 or 5 rewards, and the

risky low-value option produced either 1 or 3 rewards. The safe high-value option guaranteed 4

rewards, and the safe low-value option guaranteed 2 rewards (see Figure 4 for a schematic of the

reward contingencies and spatial layout). Except for the outcome values, Experiment 2b

employed identical methods as those used in Experiment 1b. Twenty of the forty-four

participants were excluded from the analysis due to failure to obtain 60% correct on catch trials.

Group 2: A second group of 24 participants (aged 19.4 ± 1.5 years old; 13 females) was

tested because so many participants in the first group failed the catch trials. These participants

were given the same procedure but received more explicit instructions about the choice task (see

Appendix A). All Group 2 participants passed the catch trials and were included in the analysis.

Data Analysis

The data analysis was conducted as per Experiment 1.

Results

Pigeons. Figure 5 shows the mean proportion of risky choices for high- and low-value

rewards along with the 95% confidence interval of the paired difference. In contrast to the

findings of Ludvig et al. (2014b; see Fig. 5A) and Experiment 1, pigeons (Fig. 5B) showed little

difference in risk selection between the high-value (M = .44; 95% CI [.36, .53]) and the low-

value (M = .44 [.35, .53]) choice types, $t(5)$= 0.10, p = .928, g = 0.04 [-1.25, 1.32], BF_{10} = 0.37.

Catch-trial performance (Figure 5D) showed no clear difference between choices with and

without the low-extreme outcome, $t(5)$= 1.68, p = .154, g = 0.63 [-0.69, 1.95], BF_{10} = 0.94.

Humans. In contrast to the pigeons, humans (see Figure 6) who passed the catch-trial

criterion in Group 1 chose the risky option significantly more frequently for high-value choices

(M = .62; 95% CI [.50, .74]) than low-value choices (M = .39 [.27, .51]), $t(23)$ = 2.99, p = .006, g

= 0.60 [0.01, 1.20], BF_{10} = 6.97. Humans in Group 2 exhibited similar risk preferences, selecting

the risky option more frequently for the high-value (M = .58 [.42, .74]) than the low-value

choices (M = .38 [.25, .50]), $t(23)$ = 2.57, p = 0.017, g = 0.52 [-0.07, 1.11], BF_{10} = 3.09.

Appendix B provides further detail about catch-trial performance in Groups 1 and 2.

Discussion

   This experiment demonstrated a difference in how pigeons and humans make risky

choices. When the outcomes did not include any zero values, humans continued to overweight

the extreme outcomes (selecting the risky option more for high values), whereas the pigeons did

not. Note how these pigeons were tested in the identical open-field procedure as in Ludvig et al.

(2014b), who found sensitivity to extremes with zero outcomes in pigeons (see Fig. 5A). In the

current study, the pigeons (unlike humans), did not show sensitivity to these extremes when there

were no zero outcomes. This pattern of results suggests that humans may be more sensitive to

extreme outcomes and pigeons may be more sensitive to zero outcomes.

<div align="center">Experiment 3: Pigeons</div>

   In view of the large methodological differences between the procedures used for pigeons

in Experiment 1a (operant) and 2a (open field), Experiment 3 tested groups of pigeons with and

without zero outcomes using a refinement of the operant procedure from Experiment 1a.

Subjects

   Subjects consisted of 16 racing pigeons (*Columba livia*). All, except one pigeon, had no

prior experience in risky-choice experiments. One bird, 473, had previously been in Experiment

1. Pigeons were housed in 165×69×178 cm group cages (5-8 birds per cage) in a temperature-

controlled colony room on a 12-hour light-dark cycle with free access to grit and vitamin-enriched water. Experimental sessions were run daily, six days a week, at the same time each day. Birds were maintained at approximately 80% of their free-feeding weight by post-session feeding.

Apparatus

Six custom-built 29.2 × 35.6 × 38.1 cm operant-conditioning chambers, equipped with the same monitors and touch screens used in Experiment 1a, were located inside a closed room. All the chambers contained an opaque barrier that blocked the lower third of touch screen from incidental contact by the pigeon's feet and chest. White noise fed through the monitor's built-in speakers maintained the internal sound at 65db. Two feeding ports located on the side walls contained the same food hoppers described in Experiment 1a. As in Experiment 1a, each chamber was connected to a computer, located in an adjacent room, running E-Prime 2.0 software (Psychology Software Tools, Pittsburgh, PA).

Stimuli

Experimental stimuli were six coloured circles 110 pixels (approx. 3 cm) in diameter presented against a grey background. All circles were aligned horizontally at the same vertical location on the screen (see Figure 7). Circles were filled with white, black, blue with a single black vertical line, orange with a hollow black circle, green a solid black "X", or purple with three black horizontal lines.

Procedure

Training Phase 1. Pigeons were given three 90-minute sessions of an autoshaping procedure with a Fixed-Ratio (FR) 1 contingency built in. One randomly selected (without

replacement) coloured circle was presented for 10 s. The circle remained on until the bird made a

single peck or until 10 s elapsed at which time the circle disappeared and one randomly-selected

hopper was raised, providing 1-s access to food, and then a 240-s ITI ensued.

Training Phase 2. This phase provided an FR1 contingency with a 2-s ITI; each circle

remained onscreen until it was pecked or the session timed out. Sessions contained 72 trials, and

the pigeon remained in the chamber for 90 minutes. Phase 2 lasted until a pigeon completed all

72 trials, with an average response time of less than 30 s on each circle type, for a single session.

Phase 2 lasted for a mean of 1.12 and range of 1-2 sessions.

Training Phase 3. Pigeons were randomly assigned to either a *Zero* group (n=8) or a *No-

Zero* group (n=8). For the Zero group, the choice circles provided values equivalent to those used

in Experiment 1a. For the No-Zero group, each value was increased by 1 (see Figure 7) for both

this phase and for the testing phase. Procedurally, this phase was the same as Training Phase 4 of

Experiment 1a except that it consisted of only one session of 64 single-option trials.

Testing. Testing lasted for 30 sessions, each consisting of 16 single-option trials and 48

choice trials (16 risk-preference choices and 32 catch choices), with full counterbalancing of

stimuli and values within each session presented in a randomized order. Apart from the number

of trials per session, testing proceeded as in Experiment 1a.

Data Analysis

Main effects and interactions between choice (high- and low-value) and Group (Zero and

No-Zero) manipulations were analyzed using linear mixed-effects modelling on the mean

proportion of choices made to the risky alternative during the last third of all trials. Models were

fit by maximum likelihood with subjects treated as a random effect and computed with the nlme

R package for R 3.5.1 statistical software (Pinheiro, Bates, DebRoy, Sarkar, 2018; R Core Team,

2018). An effect size in terms of r^2 is reported for each fixed-effect in the full model. Bayes

Factors (BF_{10}) are also provided for each effect and tested against a null model that included only

the intercept and an additive random effect of subject.

Simple-effects analysis on the difference between the high- and low-value choices for the

Zero and No-Zero groups were analyzed using a paired t-test. For each simple effect, a

corresponding effect-size (g) and JZS Bayes factor (BF_{10}) is provided as per Experiment 1.

Similar sets of analyses are provided for catch-trial assessment.

Results

Three birds in the No-Zero group failed to meet the 60% catch-trial criterion and were

subsequently removed from the analysis; none of the birds in the Zero group failed to reach the

criterion. Figure 8 shows the mean proportion of risky option selections for high- and low-value

choice types along with the 95% confidence interval of the paired difference for both the Zero

and No-Zero groups. Although both the Zero and No-Zero groups showed greater selection of

the risky option for high-value outcomes, $M =.48$ 95% CI [.35, .61] and $M =.57$ [.35, .79], than

low-value outcomes, $M =.10$ [.04, .17] and $M =.40$ [.24, .57], this difference was larger and less

variable in the Zero group. Statistical analysis showed a significant main effect of both choice, χ^2

(1) = 15.88, $p < .001$, $r^2 = .25$, $BF_{10} > 150$, and group, χ^2 (1) = 9.68, $p = .002$, $r^2 = .11$, $BF_{10} >$

150, as well as a significant interaction between these two variables, χ^2 (1) = 4.00, $p = .045$, $r^2 =$

.25, $BF_{10} > 150$. Consistent with our previous findings, simple-effects analysis showed a

significant difference between the high- and low-value outcomes in the Zero group, $t(7) = 5.33$, p

$= .001$, $g = 1.78$ [0.51, 3.05], $BF_{10} = 38.42$, but not in the No-Zero group, $t(4) = 2.01$, $p = .115$, g

= 0.81 [-0.71, 2.33], BF_{10} = 1.24. These results confirm that there was a larger and more reliable

difference between the high- and low-value choices in the Zero group than the No-Zero group.

Figures 7B and 7C show catch-trial performance for the Zero and No-Zero groups.

Similar to Experiment 1a, the Zero group was more accurate for choices that contained the low-

extreme value (i.e., a possibility of zero). Similar to Experiment 2a, however, this difference in

catch-trial type was not observed in the No-Zero group (where zero was not a possible outcome).

Statistical analysis confirmed a significant interaction between catch-trial type and group, χ^2 (1)

= 6.54, p = .011, r^2 = .40, BF_{10} > 10.91. Analysis of the simple-effects revealed a large difference

between choices with and without the lowest extreme for the Zero group; $t(7)$ = 4.08, p = .005, g

= 1.13 [-0.03, 2.28], BF_{10} = 11.88, but not for the No-Zero group; $t(4)$ = 0.37, p = .732, g = 0.19

[-1.27, 1.66], BF_{10} = 0.42.

Discussion

Experiment 3 manipulated the occurrence of zeros between two groups of pigeons tested

with an identical operant task. Similar to Experiment 1a, the Zero group showed a pronounced

difference between high- and low-value choices, whereas this difference was significantly

smaller and not statistically reliable for the No-Zero group. Additionally, whereas the Zero group

showed clear risk aversion for low-value choices, neither the high- nor the low-value choices in

the No-Zero group differed significantly from chance levels. These observations, in conjunction

with the imbalances between catch trials containing risky low-value and safe low-value

outcomes, support the conclusion that pigeons are more affected by a general avoidance of zero

than by an overweighting of the extremes.

Experiment 4: Discrimination Test

In Experiments 2 and 3, pigeons failed to show a significant extreme-outcome effect when none of the outcomes included a zero value. This insensitivity to the extremes may be due to an inability of the pigeons to discriminate between the outcomes when there are no zeros. Although the catch-trial data suggested that pigeons did not completely fail to discriminate, the catch trials did not explicitly test a pigeon's ability to discriminate between all possible outcomes (e.g., 4 versus 5). Experiment 4 sought to verify the conclusions of Experiments 2 and 3 by first pre-testing pigeons' ability to discriminate between all combinations of the No-Zero choice outcomes used in Experiment 3 (i.e., 1-5) and then testing those same pigeons using a variant of the Experiment 3 No-Zero procedure.

Methods

Subjects and Apparatus. Subjects consisted of 8 racing pigeons (*Columba livia*) with no prior experience in risky-choice experiments. Subjects were maintained as per Experiment 3 and run in the same experimental chambers described in Experiment 3.

Reinforcer Magnitude Discrimination. Similar to Experiment 3, pigeons were presented with coloured choice circles that led to a horizontal array of token circles, each of which required a single peck to obtain 1 s of access to food. The procedure was modified, however, to enhance discriminability of the alternatives. Five choice circles, 2 cm in diameter, were presented in a horizontal array just beneath the location of the token array (see Figure 9). Each choice circle had a fixed spatial location that was demarcated by a hollow black circle on a grey background. Each choice circle was assigned a unique colour and had a number centrally inscribed, in black Times font, that corresponded to its outcome. For instance, if a bird selected a dark green circle inscribed with a "3", that circle would disappear, and three corresponding dark

green tokens would appear above it, each of which could be pecked for 1-s access to food in any

order. The colour of the tokens always matched the respective choice circle that was selected, but

no number appeared inside. The outcome of each choice circle was fixed to a particular reward

amount (not probabilistic), and the values ranged from 1 to 5.

Two different space-colour mappings were used for the choice circles. From the leftmost

circle to rightmost circle, the colours for one mapping were golden brown, light blue, dark green,

dark yellow, and magenta. For the other spatial mapping, these same colours were offset by 2

positions to the right. Two different spatial-number mappings were also used, and, from left to

right, these were 1, 2, 3, 4, 5, and 4, 5, 1, 2, 3. Birds were randomly assigned to the resulting 4

colour-number combinations. Unlike the previous experiments, no start-stimulus was used in

Experiment 4.

Initially pigeons were tested on an FR1 condition that required only a single peck to

select a choice stimulus. This produced weak discrimination across the full range of values (see

Results section). Consequently, the birds were re-tested with the ratio requirement on the choice

stimuli increased to FR40 because increased ratio requirements have been shown to improve

accuracy in both simple and complex discrimination tasks (e.g., Elsmore, 1971; Wilkie &

Spetch, 1978). Upon beginning the FR40 condition, all but one pigeon (bird #76, described

below) were reassigned to new colour and number locations to require relearning of the

contingencies. Training and testing occurred as per Experiment 3, except that Phase 2, Phase 3,

and testing consisted of 65 trials per session to allow for complete within-session balancing of

the stimuli. Each session consisted of 15 single-option trials and 50 dual-choice trials. All choice

combinations across the outcome values were tested (e.g., 5 vs. 4, 5 vs. 3, 5 vs. 2, 5 vs. 1, 4 vs. 3, etc.) in a randomized fashion.

The FR1 condition included training Phases 1, 2, and 3; however, the FR40 condition only included training Phase 3. During Phase 3 of the FR40 condition, the ratio requirement was shaped according to a geometric progression: 1, 2, 4, 6, 9, 12, 15, 20, 25, 32, 40, with the value increasing every five trials. Pigeons remained on Phase 3 with an FR40 requirement on all trials until they completed all 65 trials within a session or three sessions had elapsed. In testing, because the high ratio requirement caused some pigeons to not complete the full 65 trials per session, each pigeon was tested until they had completed at least 1500 choice trials across the sessions. The mean number of testing sessions was 36, ranging from 30 to 55.

Risky Choice. Following the discrimination testing, pigeons were moved to the risky-choice procedure. The procedure was the same as the No-Zero group in Experiment 3, except with an FR40 response requirement. Training phases 1 and 2 were included. Four new colours were used for the choice circles and tokens: red, yellow, green, blue. Each choice circle was also inscribed with a specific letter A, B, C, or D, in black Times font. The tokens matched the colour of the selected choice stimulus and were presented above the selected circle. The choice stimuli were mapped onto a risky-high outcome, a risky-low outcome, a safe-high outcome, and a safe-low outcome. The location-colour, location-letter, and location-outcome mappings were all randomized independently according to a Latin-square design. Each bird was randomly assigned to a specific mapping on the condition that blue and yellow circles did not correspond to the same values received during the FR40 discrimination testing. Each session consisted of a maximum of 64 trials: 16 single-option, 16 choice, and 32 catch trials in a randomized order.

With the exception of one pigeon (#76), testing continued until each pigeon had completed 1440

choice trials. Bird #76, who ran for 123 sessions with a mean of 11 choice trials per session, only

completed 1294 choice trials before the experiment was ended. Across all other pigeons, the

mean number of sessions was 32, ranging from 30 to 40.

     Data Analysis. Analyses for risky choice proceeded as in the earlier experiments. For the

discrimination task, we first compared the proportion correct for the discriminations that were

only a single unit apart (e.g., 3 vs. 4), which should be the hardest discriminations for pigeons.

To better quantify the pigeons' discrimination across the 10 possible choice types in the FR1 and

FR40 conditions, we next evaluated relative preferences in terms of the generalized matching

equation (GME) as applied to reinforcer magnitude (Baum, 1974; Davison & Baum, 2003).

Given the ubiquity of matching in choice and the straightforward application and interpretation

of generalized matching relations (deVilliers, 1977), the GME offers a useful lens with which to

evaluate pigeons' choices across the full range of outcomes used in Experiment 4. Equation 1

shows the GME applied to reinforcer magnitude:

$$\log_{10} \frac{B_1}{B_2} = a \, \log_{10} \frac{M_1}{M_2} + \log_{10} k, \qquad\qquad (1)$$

where B is the number of responses emitted to a particular choice alternative, and M is the total

amount of food delivered for a given choice outcome. Subscripts refer to the different options (1

or 2). The intercept parameter k, called bias, is a measure of preference for B_1, relative to B_2,

independent of the reinforcer magnitudes. A positive bias indicates a general preference toward

the higher reward magnitude, independent of the ratio of the items. The slope parameter a,

referred to as sensitivity, indexes how the log response ratio grows with the log reinforcer

magnitude. Perfect matching to the log magnitude ratios should result in bias and sensitivity

values of 0 and 1 respectively.

The GME was fit to the last third of each pigeon's data for both the FR1 and FR40

condition using least-squares linear regression with R 3.5.1 software (R Core Team, 2018).

Because pigeons sometimes exclusively chose one option, a correction of 0.1 was added to the

numerator and denominator of each pigeon's response ratio to prevent the occurrence of zero

values. Mean bias (intercept) and sensitivity (slope) parameters are reported with corresponding

95% confidence intervals.

Results

Figure 10A shows the probability of selecting the high-value option for the four choices

that contained outcomes only 1 token apart. Across all 8 pigeons, none of the four choice types

in the FR1 condition exceeded chance levels, whereas, in the FR40 condition, all but one choice

type (4 vs 3) exceeded chance. Figure 10B displays the overall fit of the GME applied separately

to the FR1 and FR40 conditions across all tested choices. For the FR1 condition, a very slight

bias of 0.10 95% CI [-0.40, 0.61] and sensitivity of 1.28 [0.04, 2.51] to log reinforcer magnitude

ratio was observed, neither of which exceeded what would be reasonably expected by perfect

matching. By contrast, noticeable overmatching was observed in the FR40 condition, as

indicated by the high sensitivity of 2.59 [1.19, 3.99] to the log reinforcer magnitude ratio. Thus,

as the log reinforcer magnitudes became more discrepant, the pigeons' preference became even

more pronounced than would be expected had they just been matching relative responding to

relative reinforcer magnitude. More critically, however, the FR40 condition also produced a

heavy bias of 0.76 [0.22, 1.30] towards choices containing the larger reinforcement value that was significantly larger than would be predicted by either indifference or strict matching.

During risky-choice testing, only one bird (#76) failed to reach the 60% catch-trial criterion and was excluded from the remaining analyses. Figure 10C shows the mean proportion of risky option selections for high- and low-value rewards and the 95% confidence interval of the paired difference. Similar to the No-Zero groups in Experiments 2a and 3, there was no significant difference in the proportion of risky choices between the high-value ($M = .41$; 95% CI [0.09, 0.74]) and low-value ($M = .34$; [0.16, 0.52]) choice types, $t(6) = 0.409$, $p = .697$, $BF_{10} = 0.38$, $g = 0.14$ [-1.02, 1.31]. Catch-trial performance (see Figure 10D) showed no clear difference between choices with and without the low-extreme outcome, $t(6) = 0.82$, $p = .445$, $g = 0.29$ [-.88, 1.46], $BF_{10} = 0.46$.

Discussion

Experiment 4 confirmed that even when pigeons can adequately discriminate between non-zero outcomes they still show little evidence for an effect of the extreme outcomes on their risky choices. These findings complement the results from Experiment 2 and 3 and suggest that pigeons are more driven by the avoidance of zero outcomes than by avoidance of a low extreme.

The ratio requirement also played a significant role in determining the degree of discrimination exhibited by the pigeons. When choice required only a single response (FR1), pigeon preferences seemed to follow basic predictions of matching, with weak discrimination at small ratios (e.g. 5:4) and progressively stronger discrimination at larger ratios (e.g. 5:1). When the response requirement was increased to 40, bias in favor of the choice alternative with the larger reward outcome became very pronounced. This increase in bias was accompanied by an

additional increase in overall sensitivity to the reinforcement ratio. The enhanced discrimination of reinforcer magnitude when the response requirement was increased is consistent with previous findings that discrimination becomes more accurate as response effort increases (e.g., Ellesmore, 1971; Wilkie & Spetch, 1978).

Given that pigeons demonstrated good discrimination of the reward values with the FR40 requirement, Experiment 4 evaluated the predictions of the extreme-outcome effect under this condition with no zero outcomes present. Even with a high ratio requirement and high levels of discrimination, pigeons still exhibited behaviour qualitatively similar to those seen in the No-Zero groups of Experiments 2 and 3: They had similar levels of risk preference for both high-value and low-value choices (see Figure 8). The clear preference for the larger reward outcome with FR40 reinforcer magnitude discriminations and the clear preference for the high-value outcome on catch trials suggest that the pattern of choice results was not due to an inability to discriminate between non-zero outcomes.

General Discussion

The present set of results demonstrate the importance of zero, or non-rewarded options, in determining risky choice in pigeons but not people. Whereas people avoided risky options that might lead to the worst outcome in a context, pigeons primarily avoided options that led to zero or no reward. When the zero value was removed as a possible outcome, humans continued to select the risky option more often for high-value options than low-value ones, consistent with previous findings (Ludvig et al., 2014a). Pigeons, however, showed no consistent pattern in their risk preferences when the zero value was removed, despite accurate choice of high-value options over low-value options. Together, these results suggest that, in contrast to our previous

suggestion (Ludvig et al., 2014b), the strikingly similar patterns of risky choice seen by pigeons and humans may be driven by different underlying mechanisms.

In humans, there is evidence that the greater risk seeking for high-value choices than for low-value choices is driven by an overweighting of extreme outcomes (Ludvig et al., 2014a). For example, manipulating the set of outcomes in the decision context can shift risk preferences: for the same choice between a safe 20-point option and a risky option leading to 0 or 40 points, people's choices range from risk seeking to risk aversion depending on the other outcome values in the decision context (Ludvig et al., 2014a; see Madan et al., 2019). Moreover, memory tests given after the choice task reveal that people are more likely to recall the extreme outcomes first and to judge them as having occurred more frequently (Madan et al., 2014; 2017). Here, too, people were more risk seeking for high-value than low-value choices, even when no zeroes were present (Exp. 2a).

Pigeons, in contrast, were not driven by the relative extremes to the same degree. When zero (i.e., no reward) outcomes were present in Experiment 1 and 3, pigeons indeed selected the risky option more often in the high-value than low-value choices. When zero outcomes were removed in Experiments 2, 3, and 4, however, pigeons no longer showed consistently different patterns for high- and low-value choices. Thus, zero outcomes appeared to more strongly control behaviour in pigeons than people. Further research is needed to determine whether non-zero extreme outcomes play a role in pigeons' risk preferences in other situations. For example, performance could be directly compared between similar-valued choices with and without an extreme-outcome (as has been done with humans; see Madan et al., 2019). Here, in all 4 experiments, the risky options always potentially led to an extreme outcome (either high or low).

One possible reason that pigeons might be particularly driven by an avoidance of zero is suggested by the probability and delay discounting literature (e.g., Green, Myerson, & Calvert, 2010; Hayden, 2015; Hayden & Platt, 2007; Mazur, 1989; Rachlin, Logue, Gibbon, Frankel, 1986). When the low-value option provides either 2 or 0 food rewards, pigeons may treat this probabilistic reward as a variable delay to reward. For all other options some reward is provided on every trial, so, although the amount of reward varies probabilistically, the occurrence of reward is never delayed. In essence, this design may resemble a self-control task whereby the pigeon chose between a smaller immediate reward, and a larger reward that sometimes occurred after a substantial delay. In these self-control tasks, pigeons typically show steep discounting functions with rewards losing most of their subjective value within a few seconds. By contrast, humans and other apes tend to exhibit much more gradual rates of discounting and are thus not subject to such a heavy early loss of value (Stevens & Stephens, 2010). This probabilistic interpretation could account for the observed differences in the pigeons' risky choice for high- and low-value options (e.g., Exp. 1a, Zero Group in Exp. 3; Ludvig et al., 2014b). The pigeons' risk neutrality observed when all outcomes provided some reward (e.g., Exp. 2a, No-Zero Group in Exp. 3, and Exp. 4) is also consistent with this interpretation. Another possibility that merits future exploration is that zero may simply be functioning as an especially potent extreme (as opposed to delay) in certain species, such as pigeons, and certain contexts, such as all gains.

The pigeons' aversion to options that sometimes provide zero outcomes is interesting in relation to evidence from other procedures showing that pigeons are sometimes drawn to options that provide food less reliably (e.g., Belke & Spetch, 1994; Dunn & Spetch 1990; Kendall, 1974; Pisklak, McDevitt, Dunn, & Spetch, 2015, Stagner & Zentall 2010). In those studies, choice was

followed by a lengthy delay (10 s or greater) during which the stimuli present indicated whether

the food would or would not occur. Stimuli which provided clear signals for food functioned as

strong conditioned reinforcers of choice, whereas stimuli that provided ambiguous or redundant

signals did not (McDevitt, Dunn, Spetch, & Ludvig, 2016). Given this importance of the

conditioned reinforcer, an interesting question is what would happen if the zero outcomes used in

Experiment 1 were preceded by a unique token that provided nothing for its selection. In this

case, the zero outcome would no longer be marked by the absence of any feedback cues. The

strong effects of the zero outcome might become attenuated – or perhaps even reversed if the

response requirement on them is greater as in studies of suboptimal choice.

One central difference between the pigeon and human experiments concerns the nature of

the terminal reinforcer. For the pigeons it was food–an unconditioned reinforcer–and for the

humans it was money–a highly generalized conditioned reinforcer. When pigeons and humans

are given tokens that have to be immediately exchanged for unconditioned reinforcers, their

sensitivity to risky delays is similar (Lagorio & Hackenberg, 2010). When both species are

forced to accumulate tokens, thereby delaying the unconditioned reinforcer, risk sensitivity

decreases. Thus, it might be predicted that forcing pigeons to accumulate tokens, as opposed to

having them exchange them immediately, might bring their results into closer alignment to those

observed for humans. Conversely, giving humans an immediate unconditioned reinforcer may

foster preferences more like those observed for pigeons.

An interesting test of the power of zero values in driving choice would be to provide

pigeons with a risky option that offers food values of 0 or 4 over a safe option that offers a value

of 1. In this case, the risky option would be the better choice in terms of overall expected value,

raising the question: would an avoidance of zero still dominate the pigeons' choice behaviour? In a two-alternative choice, the answer appears to be yes. For example, Menlove, Inden, and Madden (1979) gave pigeons a choice between a key that delivered a fixed 2 seconds of food and a key that gave pigeons either 8 or zero seconds of food. All pigeons preferred the fixed option, suggesting an avoidance of zero would dominate in this hypothetical experiment. What remains uncertain, however, is whether these results would generalize to a situation where the decision context contains additional higher-value choice alternatives (e.g., a choice between 0 or 4 versus 1 and a choice between 2 or 6 versus 3). Given that the current results suggest pigeons are not especially sensitive to the extreme outcomes in such contexts, avoidance of zero would likely still occur.

The present results suggest that pigeons are particularly sensitive to zero outcome values, especially in comparison to human participants, and it is interesting to speculate on why. As we have discussed, zero values could transform the task into one that taps into delay discounting, bringing pigeons' steep discounting functions into play. The use of consumable reinforcement for hungry pigeons could also make zero values particularly salient or memorable; not eating at all may be qualitatively not just quantitatively different than not eating. It is also possible that pigeons (and potentially many other species) have evolved to be highly sensitive to the absence of an important outcome, and perhaps less so to the quantity of that outcome as long as some is obtained. For example, it could be adaptive to remember choices that sometimes lead to no food because in cases of severe food shortage, obtaining nothing could risk starvation. All of these speculations will require further experimentation with other tasks, types of reinforcement, and species.

The present research provides a striking example of how behavioural similarities across species need not be indicative of the same underlying mechanism. Although humans and pigeons chose similarly to the options presented in Experiment 1, which included a zero value (and in Ludvig et al., 2014b), their choices were quite different when the zero outcome was removed in Experiment 2, 3, and 4. Avoiding the zero value played a very powerful role in controlling the risky choices of pigeons, but not humans. Comparative research between humans and other animal species has been remarkably successful in delineating many robust and highly important behavioural processes that generalize across numerous species—e.g., schedules of reinforcement, hyperbolic discounting, equivalence class formation, and generalized matching, to name just a few. This work, however, provides an important cautionary tale about the challenges of effective comparative research, whereby some similarities may, paradoxically, not actually be the same.

References

Barnard, C. J., Brown, C. A. J., Houston, A., & McNamara, J. M. (1985). Risk-sensitive foraging

in common shrews: An interruption model and the effects of mean and variance in reward

rate. *Behavioral Ecology and Sociobiology, 18*, 139-146. doi:10.1007/BF00299042

Barron, G., & Erev, I. (2003). Small feedback-based decisions and their limited correspondence

to description-based decisions. *Journal of Behavioral Decision Making*, *16*, 215-233.

doi:10.1002/bdm.443

Bateson, M., & Kacelnik, A. (1995). Preferences for fixed and variable food sources: Variability

in amount and delay. *Journal of the Experimental Analysis of Behavior, 63*(3), 313–329.

Baum, W. M. (1974). On two types of deviation from the matching law: Bias and

undermatching. *Journal of the Experimental Analysis of Behavior*, *22*(1), 231–242.

doi:10.1901/jeab.1974.22-231

Camilleri, A. R., & Newell, B. R. (2011). Description-and experience-based choice: Does

equivalent information equal equivalent choice?. *Acta Psychologica*, *136*(3), 276-284.

doi:10.1016/j.actpsy.2010.11.007

Caraco, T., Martindale, S., & Whittam, T. S. (1980). An empirical demonstration of risk-

sensitive foraging preferences. *Animal Behaviour*, *28*(3), 820-830. doi:10.1016/S0003-

3472(80)80142-4

Constantinople, C. M., Piet, A. T., & Brody, C. D. (2018). An Analysis of Decision Under Risk

in Rats. *bioRxiv*, 446575. doi: 0.1101/446575

Davison, M., & Baum, W. M. (2003). Every reinforcer counts: reinforcer magnitude and local

    preference. *Journal of the Experimental Analysis of Behavior*, *80*(1), 95–129.

    doi:10.1901/jeab.2003.80-95

deVilliers, P. A. (1977). Choice in concurrent schedules and a quantitative formulation of the law

    of effect. In W. K. Honig & J. E. R. Staddon (Eds.), *Handbook of Operant Behavior*.

    New York: Prentice Hall, 1977.

Elsmore, T. F. (1971). Effects of response effort on discrimination performance. *Psychological

    Record, 21*(1), 17-24, doi:10.1007/BF03393984

Franz, V., & Loftus, G. (2012). Standard errors and confidence intervals in within-subjects

    designs: Generalizing Loftus and Masson (1994) and avoiding the biases of alternative

    accounts. *Psychonomic Bulletin & Review*, *19*(3), 395–404. doi:10.3758/s13423-012-

    0230-1

Green, L., Myerson, J., & Calvert, A. (2010). Pigeons' discounting of probabilistic and delayed

    reinforcers. *Journal of the Experimental Analysis of Behavior*, *94*(2), 113-123.

    doi:10.1901/jeab.2010.94-113

Hayden, B. Y. (2015). Time discounting and time preference in animals: A critical review.

    Psychonomic Bulletin & Review. *23*(1), 39-53. doi:10.3758/s13423-015-0879-3

Hayden, B. Y., Heilbronner, S. R., Nair, A. C., & Platt, M. L. (2008). Cognitive influences on

    risk-seeking by rhesus macaques. *Judgment and Decision Making*, *3*(5), 389-395.

Hayden, B.Y., & Platt, M.L., (2007). Temporal discounting predicts risk preferences in monkeys.

    Current Biology, *17*(1)*,* 49-53. doi:10.1016/j.cub.2006.10.055

Hayden, B. Y., & Platt, M. L., (2009). Gambling for Gatorade: Risk-sensitive decision making

for fluid rewards in humans. *Animal Cognition*, *12*(1), 201-207. doi:10.1007/s10071-008-

0186-8

Heilbronner, S. R., & Hayden, B. Y. (2016). The description-experience gap in risky choice in

nonhuman primates. *Psychonomic bulletin & review*, *23*(2), 593-600.

doi:10.3758/s13423-015-0924-2

Hertwig, R., & Erev, I. (2009). The description–experience gap in risky choice. *Trends in

Cognitive Sciences*, *13*(12), 517-523. doi:10.1016/j.tics.2009.09.004

Hothorn, T., Hornik, K., van de Wiel, M. A., Winell, H., & Zeileis, A. (2008). Coin: Conditional

Inference Procedures in a Permutation Test Framework. R. package version 1.2-2.

http://coin.r-forge.r-project.org/

Kahneman, D., & Tversky, A. (1979). Prospect theory: An analysis of decision under risk.

Econometrica, *47*(2), 263-291. doi:10.2307/1914185

Lagorio, C., & Hackenberg, T. (2010). Risky choice in pigeons and humans: A cross-species

comparison. *Journal of the Experimental Analysis of Behavior*, *93*(1), 27-44. doi:

10.1901/jeab.2010.93-27

Lagorio, C., & Hackenberg, T. (2012). Risky choice in pigeons: Preference for amount

variability using a token-reinforcement system. *Journal of the Experimental Analysis of

Behavior*, *98*(2), 139-154. doi:10.1901/jeab.2012.98-139

Ludvig, E. A., & Spetch, M. L. (2011). Of black swans and tossed coins: Is the description-

experience gap in risky choice limited to rare events. *PLOS ONE*, *6.*

doi:10.1371/journal.pone.0020262

Ludvig, E. A., Madan, C. R., & Spetch, M. L. (2014a). Extreme outcomes sway risky decisions

	from experience. *Journal of Behavioral Decision Making*, *27*, 145-156.

	doi:10.1002/bdm.1792

Ludvig, E. A., Madan, C. R., Pisklak, J. M., & Spetch, M. L. (2014b). Reward context

	determines risky choice in pigeons and humans. *Biology Letters*, *10*(8).

	doi:10.1098/rsbl.2014.0451

Madan, C. R., Ludvig, E. A., & Spetch, M. L. (2014). Remembering the best and worst of times:

	Memories for extreme outcomes bias risky decisions. *Psychonomic Bulletin and Review*,

	21(3), 629-636. doi:10.3758/s13423-013-0542-9

Madan, C. R., Spetch, M. L., & Ludvig, E. A. (2015). Rapid makes risky: Time pressure

	increases risk seeking in decisions from experience. *Journal of Cognitive

	Psychology*, *27*(8), 921-928. doi:10.1080/20445911.2015.1055274

Madan, C. R., Ludvig, E. A., & Spetch, M. L. (2017). The role of memory in distinguishing risky

	decisions from experience and description. *The Quarterly Journal of Experimental

	Psychology*, *70*(10), 2048-2059. doi:10.1080/17470218.2016.1220608

Madan, C. R., Ludvig, E. A., & Spetch, M. L. (2019). Comparative Inspiration: From puzzles

	with pigeons to novel discoveries with humans in risky choice. *Behavioral Processes*,

	160, 10-19. doi: 10.1016/j.beproc.2018.12.009

Marsh, B., & Kacelnik, A. (2002). Framing effects and risky decisions in starlings. *Proceedings

	of the National Academy of Sciences*, *99*(5), 3352-3355. doi: 10.1073/pnas.042491999

Mazur, J. E. (1984). Tests of an equivalence rule for fixed and variable reinforcer delays. *Journal of Experimental Psychology: Animal Behavior Processes, 10*(4), 426-436. doi: 10.1037//0097-7403.10.4.426

Mazur, J. E. (1986). Fixed and variable ratios and delays: Further tests of an equivalence rule. *Journal of Experimental Psychology: Animal Behavior Processes, 12*(2), 116-124. doi:10.1037/0097-7403.12.2.116

Mazur, J. E. (1989). Theories of probabilistic reinforcement. *Journal of the Experimental Analysis of Behavior*, *51*(1), 87-99. doi:10.1901/jeab.1989.51-87

Marshall, A. T., & Kirkpatrick, K. (2013). The effects of the previous outcome on probabilistic choice in rats. *Journal of Experimental Psychology-Animal Behavior Processes*, *39*(1), 24-38. doi:10.1037/a0030765

McDevitt, M.A., Dunn, R.M., Spetch, M.L., & Ludvig, E.A. (2016). When good news leads to bad choices. *Journal of the Experimental Analysis of Behavior. 105*(1), 23-40. doi:10.1002/jeab.192

Menlove, R. L., Inden, H. M., & Madden, E. G. (1979). Preference for fixed over variable access to food. *Animal Learning and Behavior*, *7*(4), 499-503. doi:10.3758/BF03209709

Morey, R. D. & Rouder, J. N. (2011). Bayes Factor approaches for testing interval null hypotheses. *Psychological Methods, 16*(4), 406-419. doi:10.1037/a0024377

Morey R. D., & Rouder, J. N. (2018). BayesFactor: Computation of Bayes Factors for Common Designs. *R package version 0.9.12-4.2.* https://CRAN.R-project.org/package=BayesFactor

Nieder, A. (2016). Representing something out of nothing: The dawning of zero. *Trends in*

    Cognitive Sciences. 20(16), 830-842. doi:10.1016/j.tics.2016.08.008

Pisklak, J. M., McDevitt, M. A., Dunn, R. M., & Spetch, M. L. (2015). When good pigeons

    make bad decisions: Choice with probabilistic delays and outcomes. *Journal of the*

    Experimental Analysis of Behavior, 104(3)*,* 241-251. doi: 10.1002/jeab.177

R Core Team (2018). R: A language and environment for statistical computing. R Foundation for

    Statistical Computing, Vienna, Austria. https://www.R-project.org/.

Rachlin, H., Logue, A., Gibbon, J., & Frankel, M. (1986). Cognition and behavior in studies of

    choice. *Psychological Review*, *93*(1), 33-45. doi:10.1037/0033-295X.93.1.33

Stagner, J. P., & Zentall, T. R. (2010). Suboptimal choice behavior by pigeons. *Psychonomic*

    Bulletin & Review, 17(3), 412-416. doi:10.3758/PBR.17.3.412

Stephens, D. W. (1981). The logic of risk-sensitive foraging preferences. *Animal Behavior.*

    29(2), 628-629. doi:10.1016/S0003-3472(81)80128-5

Stevens, J. R., & Stephens, D. W. (2009). The adaptive nature of impulsivity. In G. J. Madden &

    W. K. Bickel (Ed.), The Behavioral and Neurological Science of Discounting (pp. 361-

    388). Washington, DC: American Psychological Association.

Torchiano (2017). effsize: Efficient Effect Size Computation*. R package version 0.7.1.*

    https://CRAN.R-project.org/package=effsize

Ungemach C., Chater, N., & Stewart, N. (2009). Are probabilities overweighted or

    underweighted when rare outcomes are experienced (rarely)? *Psychological Science.*

    20(4). 473-479. doi:10.1111/j.1467-9280.2009.02319.x

Wilkie, D. M., & Spetch, M. L. (1978). The effect of sample and comparison ratio schedules on

delayed matching to sample in the pigeon. *Animal Learning & Behavior*, *6*(3), 273-278.
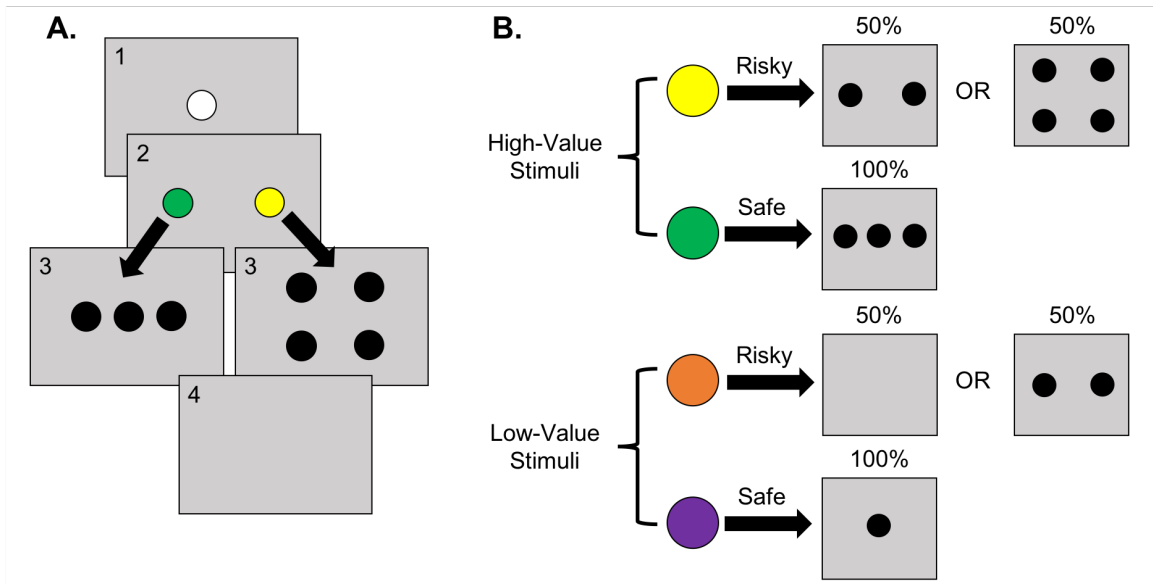
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Figure 1. (A) A schematic of a choice trial displaying a risky high-value option and a safe high-value option, with possible outcomes in Experiment 1. (B) A schematic illustrating the various reward contingencies in effect. The colour of the choice circles relative to their outcome was counterbalanced across participants according to four different combinations of yellow, green, orange, and purple.
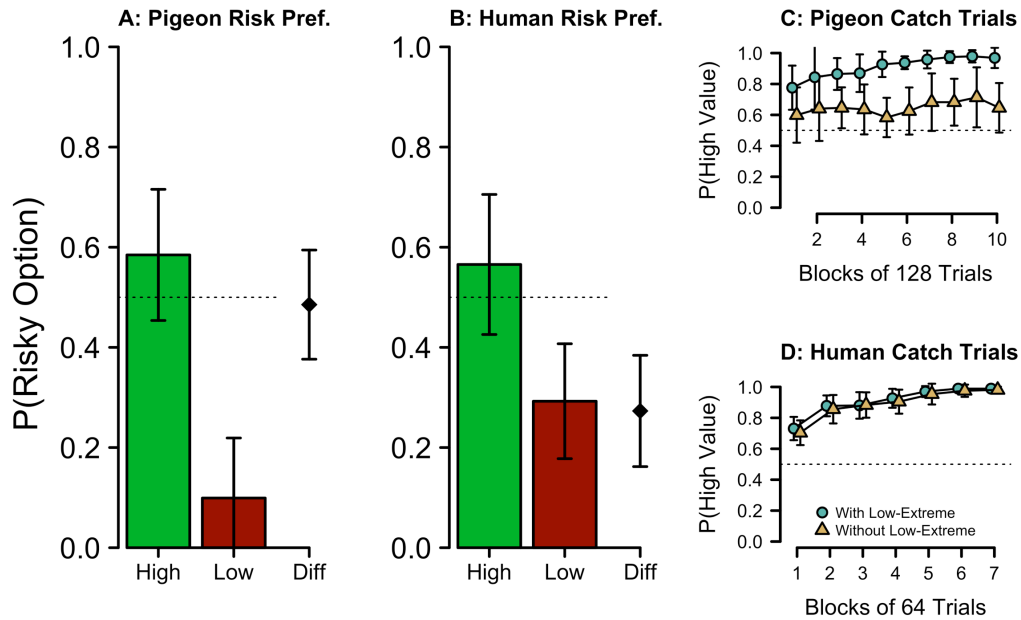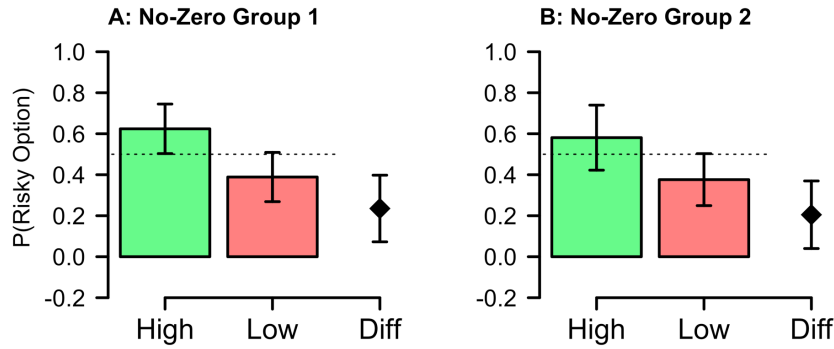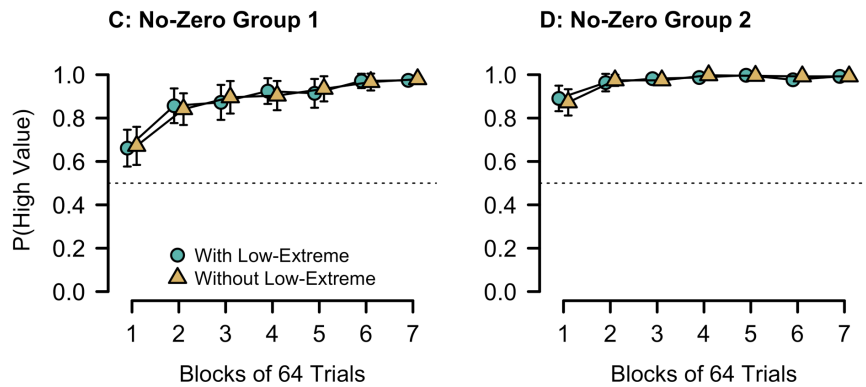
Figure 2. Probability of choosing the risky option for (A) pigeons and (B) humans on high- and low-value risk preference trials in Experiment 1. The mean difference is shown on the right of each plot. Catch trial learning curves for (C) pigeons and (D) humans in Experiment 1 that passed the 60% threshold. The curves depict the proportion of choices made to the high-value option for catch trials containing the low-extreme outcome (i.e., possibility of receiving zero) and catch trials without the low-extreme outcome (i.e., no possibility of receiving zero). All error bars indicate 95% confidence intervals. Dotted lines indicate chance levels.
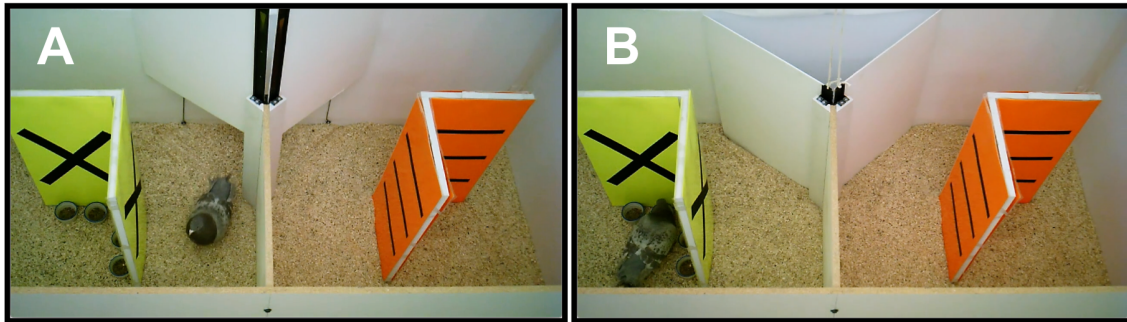
Figure 3. The testing arena during an example trial in Experiment 2a. (A) Pigeon entering the decision area via the open doors. (B) Pigeon eating from the food cups concealed behind the choice stimulus.
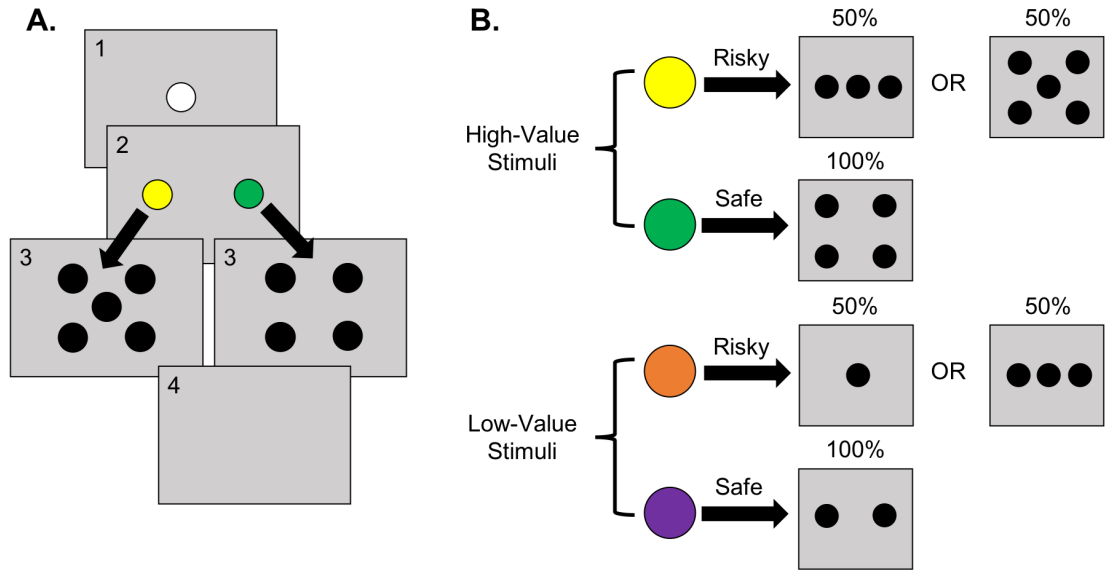
Figure 4. Schematics of the procedure for Experiment 2b. (A) Choice trial procedure, displaying a potential outcomes from a risky high-value choice and a safe high-value choice. (B) Illustration of the reward contingencies in effect. The colour of the choice circles relative to their outcome was counterbalanced across participants according to four different combinations of yellow, green, orange, and purple.
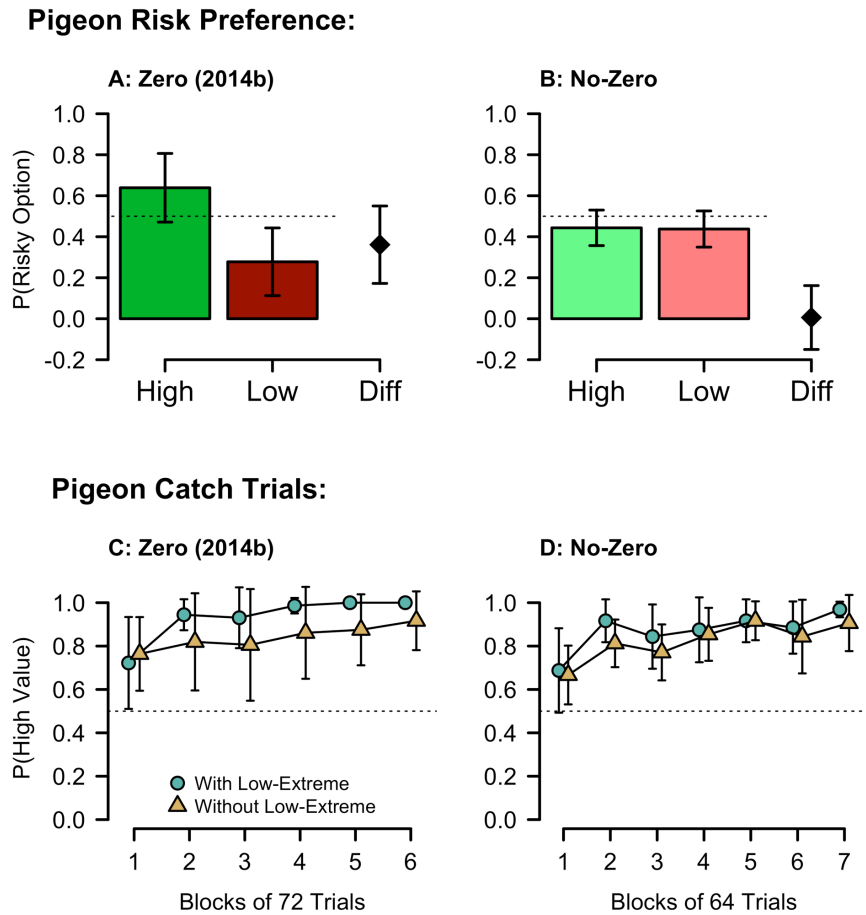
Figure 5. Pigeon choice data from Ludvig et al. (2014b) and Experiment 2. (A-B) Proportion of

risky option selections for high- and low-value choice trials. The mean difference is shown on

the right of each plot. (C-D) Proportion of choices made to the high-value option for catch trials

with the low-extreme and catch trials without the low-extreme. All error bars indicate 95%

confidence intervals. Dotted lines indicate chance levels.

Human Risk Preference:

Figure 6. Human choice data Experiment 2. (A-B) Proportion of risky option selections for high- and low-value choice trials. The mean difference is shown on the right of each plot. (C-D) Proportion of choices made to the high-value option for catch trials with the low-extreme and catch trials without the low-extreme. All error bars indicate 95% confidence intervals. Dotted lines indicate chance levels.
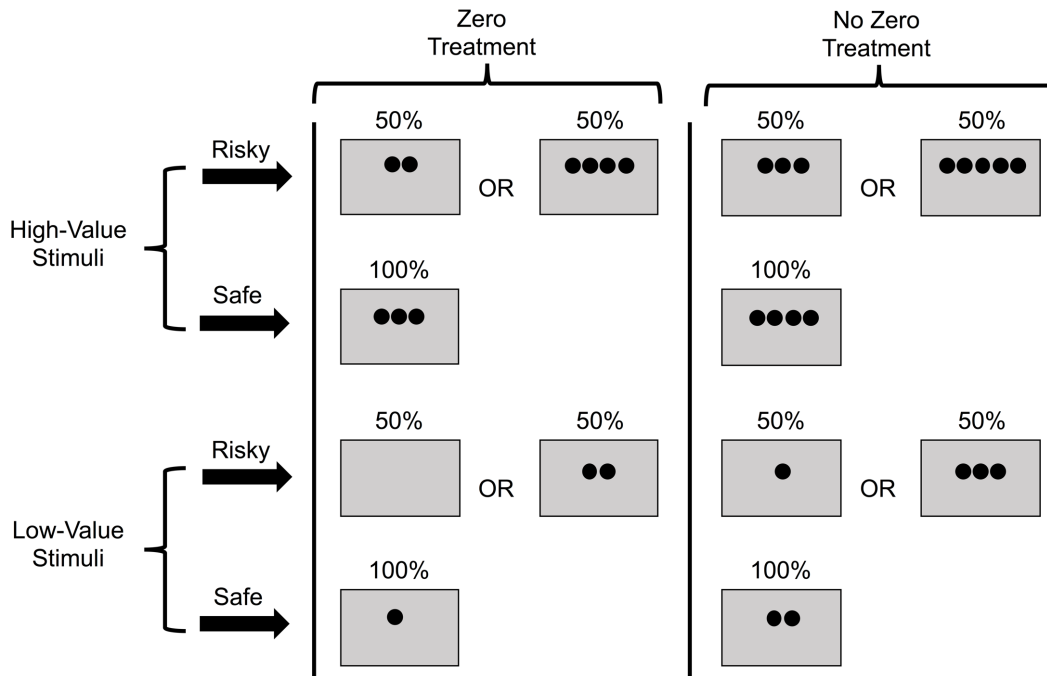
Figure 7. A schematic illustrating the various reward contingencies in effect for the Zero and
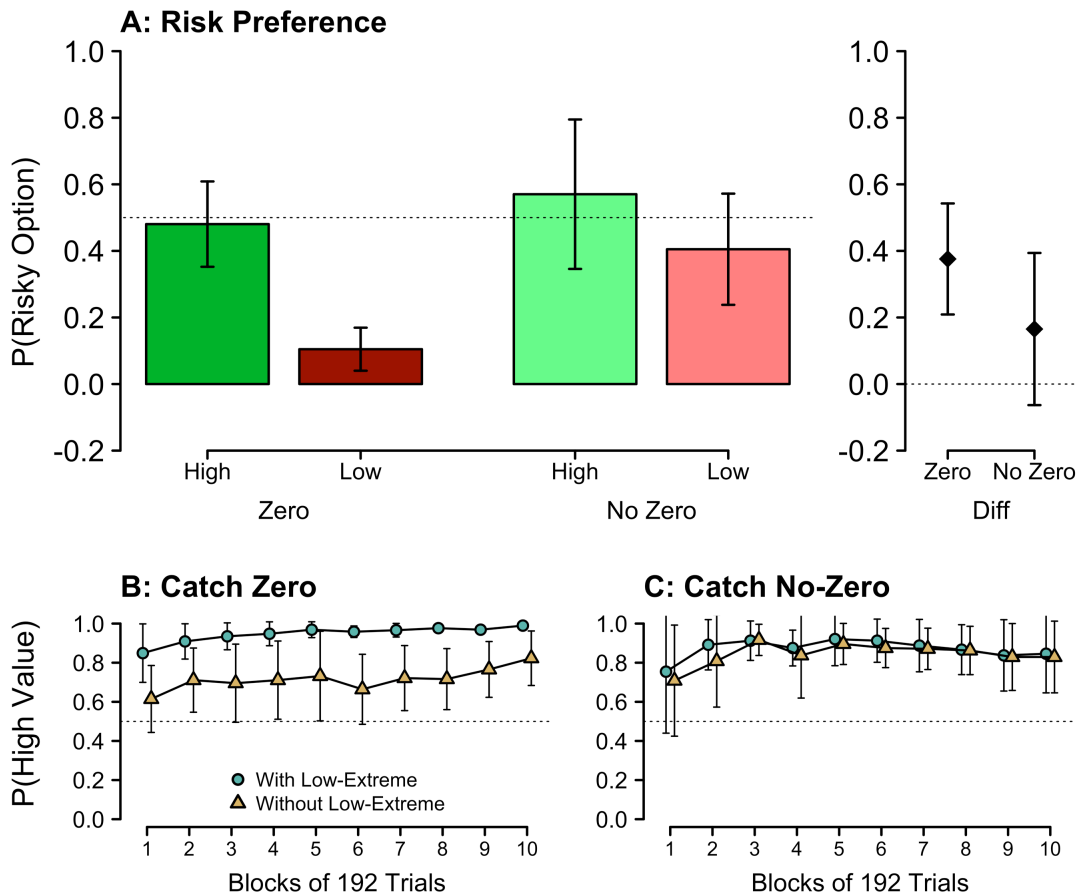
No-Zero groups in Experiment 3.

Figure 8. Choice data from the Zero and No-Zero groups in Experiment 3. (A) Probability of

choosing the risky option for pigeons on high- and low-value risk preference trials. The right

panel shows the mean difference between high- and low-value proportions for both groups.

Catch trial learning curves for the (B) Zero and (C) No-Zero groups for pigeons passing the 60%

threshold. The curves depict the proportion of choices to the high-value option for catch trials

with and without the lowest extreme outcome. All error bars indicate 95% confidence intervals.

Dotted lines indicate chance levels.
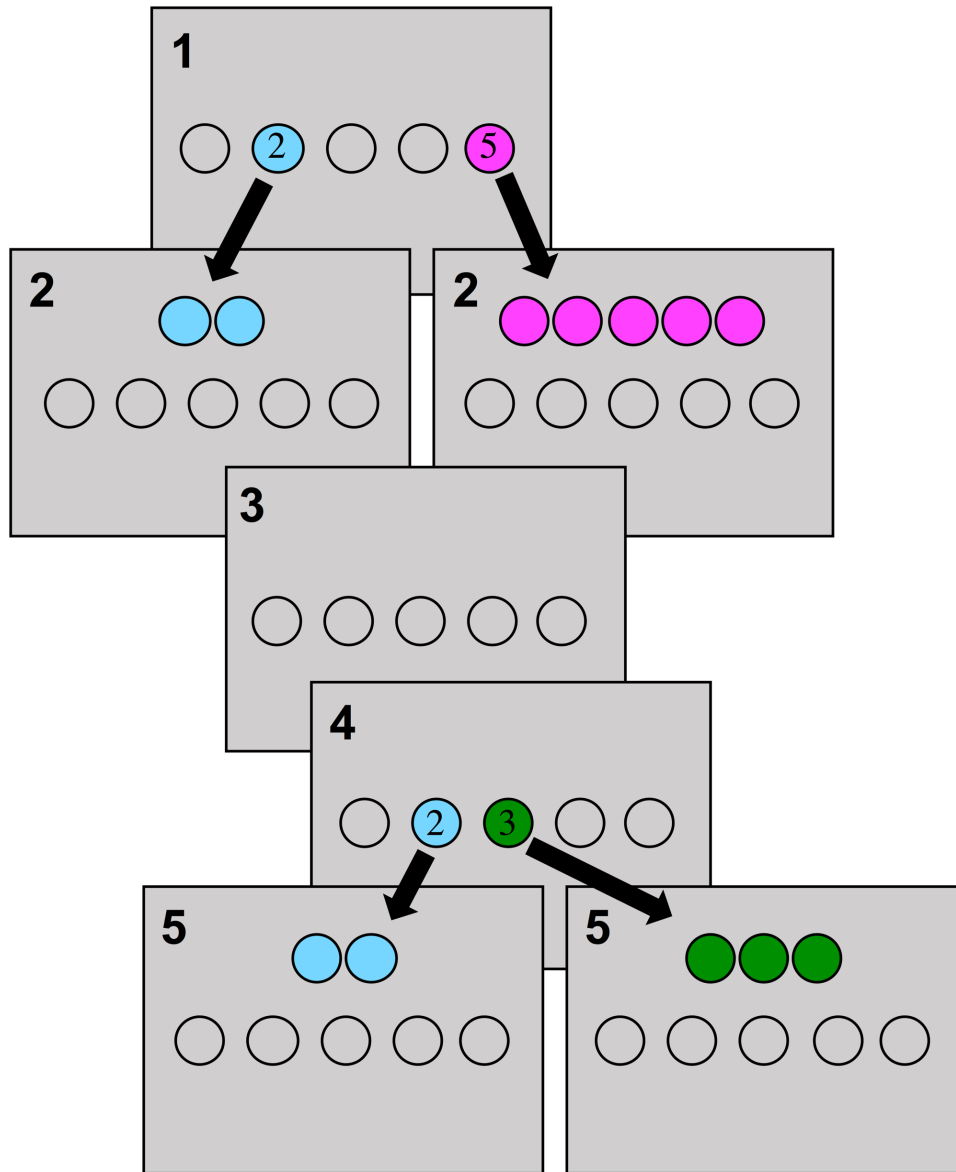
Figure 9. A schematic of two choice trials on Experiment 4's reinforcer amount discrimination training. Panel 1 and 4 show two of ten possible choice scenarios pigeons were given. Panel 2 and 5 show the resulting token outcomes of each choice. Panel 3 shows the inter-trial interval.
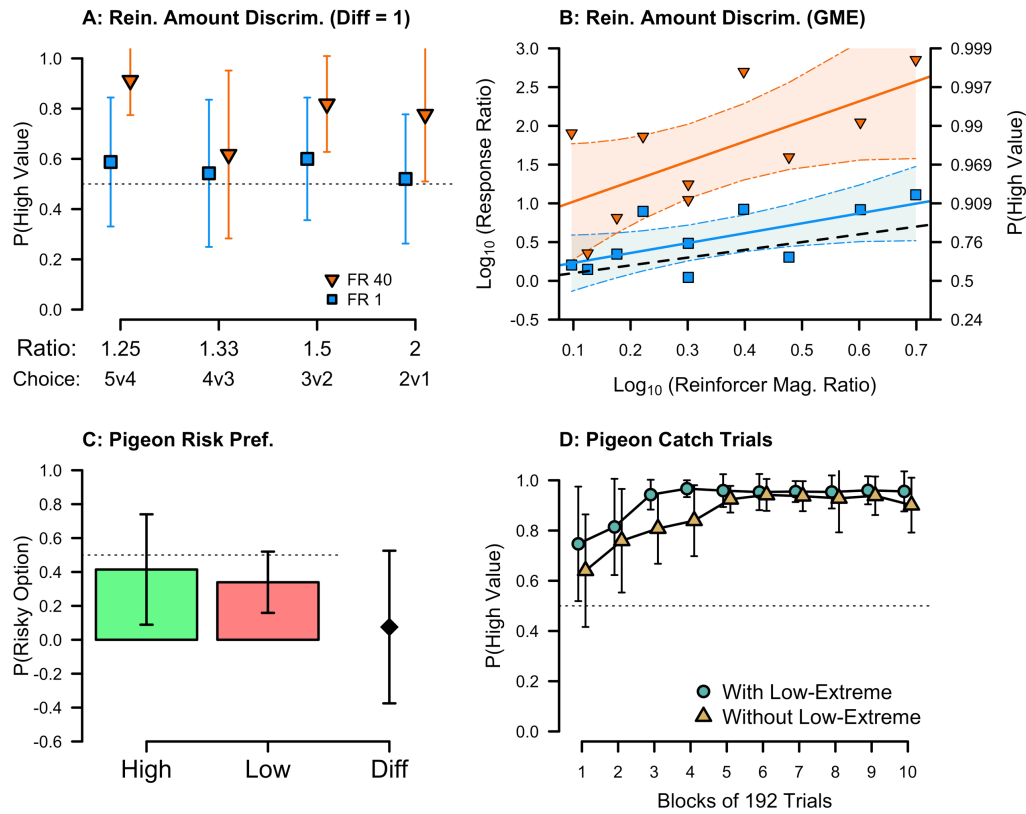
Figure 10. Panels A and B show the results of Exp. 4's discrimination testing in all pigeons

(n=8). (A) The probability of selecting the high-value option for choices that differed by only

one token. (B) The matching relation between the log response ratio (high/low) on the left y-axis

and the log reinforcer magnitude ratio (high/low) on the x-axis. Right-side y-axis shows

proportion of high-value responses on a log scale. Blue and orange regression lines indicate FR1

and FR40 condition respectively, dashed line indicates perfect matching. Panels C and D show

the results of risky-choice testing from pigeons that passed the catch trial criterion (n= 7). Error

bars and regression confidence bands are calculated at a 95% level. Dotted lines indicate chance

levels.

Appendix A

The following instructions were read aloud and projected onto a lecture screen:

Instructions for Experiment 1b and Experiment 2b - Group 1

The experiment consists of a computer portion and a maze portion. For the computer portion use the mouse cursor to click on the circles that you see. Try and get as many points as possible. For the maze portion a message will appear on screen telling you when to complete a particular maze. Take a few minutes to complete the maze with a pen or pencil. All the mazes are solvable, but don't worry if you can't solve it. The experiment should take just under 2 hours to complete. You will earn 2 credits for participating, and receive a cash bonus of up to $5.00 depending upon the number of points you get in the computer portion. The more points you get the more money you will earn.

Instructions for Experiment 2b – Group 2

The experiment consists of a computer portion and a maze portion. For the computer portion your goal is to earn as many points as you can. After clicking on a white centre circle, you will see one or two coloured circles on the computer screen. You choose a coloured circle by clicking on it with the mouse. After clicking the coloured circle you will see one or more black circles, clicking each black circle will give you one point. When there are two circles you should choose the one you think will win you the most black circles (i.e., the most points). If there is only one circle on the screen, you must click on that one circle to continue. For the maze portion a message will appear on screen telling you when to complete a particular maze. Take a few minutes to complete the maze with a pen or pencil. All the mazes are solvable, but don't worry if you can't solve it. The experiment should take just under 2 hours to complete. You will earn 2

credits for participating and receive a cash bonus of up to $5.00 depending upon the number of

points you get in the computer portion. The more points you get the more money you will earn.

Appendix B

Although risk preference was highly similar across Group 1 and Group 2, the percentage

of participants who passed the catch trials was strikingly different−only 55% of the 44

participants in Group 1 (who received minimal instructions) compared to 100% of the 24

participants in Group 2 (who received more detailed instructions). A Pearson's Chi-squared test

showed this difference between groups to be statistically significant, $\chi^2(1) = 15.45$, $p < .001$, $d =$

1.08 [0.52, 1.63].

The subset of participants in Group 1 who passed the catch trials scored near ceiling,

while the subset of participants who failed the catch trials consistently scored near chance. One

possibility is that participants who failed the catch trials had attempted to maximize rewards by

responding as quickly as possible. Indeed, those who failed the catch trials typically responded

faster (*Mdn* = 488 ms, IQR [460, 569]) than those who passed the catch trials (*Mdn* = 738 ms

[679, 874]). This difference was significant (*Z* = 4.91, *p* < .001) according to a *post-hoc* a

randomization test performing 10,000 Monte Carlo re-samplings of the median choice response

times using the Coin R package (Hothorn, Hornik, van de Wiel, Winell, & Zeileis, 2006).

Among participants who passed the catch-trial criterion, no significant differences were

observed in catch-trial performance for trials with and without the low-extreme outcome for

either Group 1 (*t*(23)= 1.16, *p* = .256, *g* = -0.23 95% CI [-0.82, 0.35], BF_{10} = 0.39) or Group 2

(*t*(5)= 1.11, *p* = .278, *g* = -0.22 [-0.81, 0.36], BF_{10} = 0.37).