Friends aren't food: pinyon jays show distinct context dependent numerical cognitive processes

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Abstract

Animals must often discriminate different quantities of objects in their environment, from numbers of food items to conspecifics. Yet we know little about how numerical cognitive abilities compare across different object types. Based on past research, we would expect individuals to use both the numerical difference (large − small) and numerical ratio (small/large) between two numbers of objects to choose between them. This study investigates whether numerical difference and ratio predict preferences for two types of stimuli, food items and conspecifics in pinyon jays (*Gymnorhinus cyanocephalus*). Subjects (N=12 for food experiment, N=20 for social experiment) chose between two food items or two group sizes for pairs of numbers between 1 and 6. In the food experiment, pinyon jays showed an overall preference for the larger option over the smaller option. Pinyon jays also chose larger numbers of items more when numerical differences were large and numerical ratios were small. However, numerical difference and ratio did not influence food choice independently. In the social experiment, we observed very different results. When choosing between sets of conspecifics, pinyon jays did not prefer the larger over smaller group sizes. Birds also did not show numerical difference or ratio effects. One rationale for these results are pinyon jays use different processes when deciding between numbers of food items and flock mates. While number was important for selecting food items, other factors such as flock mate identity may be more important for selecting social groups to join. Thus, in numerical preference situations, the type of objects offered can drive the numerical processes that animals use.

Keywords: Corvid, Difference, Number, Quantity, Ratio
Word count:

Introduction

Many animal species have demonstrated the ability to quantify objects in their environment, including arthropods [1], fish [2–4], amphibians [5], birds [6–8], and mammals [9–12]. Quantification skills have strong adaptive value for survival and reproduction [10], playing a role in navigation, predator avoidance, territory defense, foraging, courtship, and mating [13–18]. Yet it remains unclear if the same cognitive processes apply across these different adaptive problems.

One of the key cognitive processes proposed for quantification is the *approximate number system*, which involves the approximate estimation of numerical quantity without relying on language or symbols [16,19]. The approximate number system is characterized by the numerical magnitude effect and the numerical distance effect [20,21]. The *numerical distance effect* asserts that discrimination improves with increasing numerical difference (i.e., the mathematical difference between two numbers: 4$-$2 has a difference of 2) between two values. Essentially, discrimination becomes easier as the difference increases and the options become more dissimilar. The *numerical magnitude effect* asserts that, at a given numerical difference, discrimination worsens with increasing magnitude, which is equivalent to a decreasing numerical ratio (the mathematical quotient between two numbers: 2/4 has a ratio of 0.5). Essentially, discrimination becomes more difficult as the numerical ratio approaches 1 and the options become more similar. Taken together, these two effects describe Weber's Law [16], which indicates the use of approximate amounts rather than precise numbers.

Animals are sensitive to quantification across a range of object types [22,23]. Most of the tasks designed to measure numerical discrimination use food as quantifiable objects [11,12,24–26]. In line with the numerical distance effect, animals typically discriminate food quantities better when there are larger numerical differences [20,24,27,28]. Similarly, the numerical magnitude effect has been supported when accuracy in food quantity discrimination decreases as the ratio between the values approaches 1 [20,29–32].

In addition to food, a subset of studies in fish have used numbers of conspecifics to assess quantification [2,33,34]. Many species prefer to be in larger groups, presumably because this dilutes their probability of being captured by predators [35,36]. Though some studies show an effect of both difference and ratio on social quantity preference [2,3], others only show an effect of ratio [33,37]. While research shows ratio and difference effects on quantification within fish populations, little research has examined conspecific numerical choices in other social systems.

The primary aim of the present study was to investigate how pinyon jays (*Gymnorhinus cyanocephalus*) use quantity information, specifically numerical difference and ratio, to choose

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between different quantities of food items or conspecifics. To address this aim, we offered pinyon jays a series of choices between smaller and larger numbers of items: either food or conspecifics. Our first hypothesis posits that pinyon jays will, on average, prefer larger over smaller numbers of food items and conspecifics. Our second hypothesis posits that pinyon jays will prefer more items when the quantities have higher numerical differences and lower numerical ratios. Our third hypothesis posits that both numerical difference and ratio will influence preference independently of each other. This distinction is important because difference and ratio are highly related: as difference increases, ratio decreases. Testing these hypotheses in two different object types investigates whether the same cognitive processes generalize across adaptive problems.

Methods

We conducted both a food experiment and a social experiment to investigate quantification of food and conspecifics. Each experiment was replicated with two sets of birds, where most birds experienced both the food and social experiment. Additional methods, data analysis, and visuals are available in the supplementary material.

Subjects

Replicate 1: Eight pinyon jays (1 female) completed all rounds of the food experiment and 10 jays (4 female) completed all rounds of the social experiment. A further 17 jays (6 female) from the colony were used as stooge conspecifics in the social experiment. Two jays were dropped from the social experiment due to unrelated health concerns.

Replicate 2: Four pinyon jays (1 female) completed all rounds of the food experiment and 10 jays (1 female) completed all rounds of the social experiment. A further 12 jays (5 female) from the colony were used as stooge conspecifics in the social experiment.

The jays in the food experiment were housed in pairs, while the jays in the social experiment were individually housed. The subjects were not food restricted in either experiment.

Food Experiment

Apparatus. The food experiment was conducted in a bird cage (72 x 48 x 48 cm) with three perches. The cage abutted a plastic stand with sliding trays that had dishes attached that could contain mealworms (Figure S1).

Experimental Procedure. At the beginning of each trial, the experimenter placed the appropriate number of mealworms in each of the dishes. The subject hopped forward to one of the front perches to signal choice. The experimenter then removed the opposite dish and the subject had up to three minutes to consume the mealworms. Once the subject consumed all mealworms, the next trial began. Subjects experienced up to X trials per session and up to X trials per day. If the subject did not make a choice and/or did not finish all mealworms within three minutes, the session stopped.

81 Each bird experienced 10 repetitions for each of the 15 numerical pairs between 1 and
82 6 (e.g., 6 vs 5, 6 vs 4, 6 vs 3, etc.). The side of the larger option was pseudo-randomized
83 with no left or right runs longer than three in a row. Subjects ran in a randomized order
84 each day.

Social Experiment

86 **Apparatus.** The apparatus was a Y maze where the subject entered a large chamber
87 at the base of the maze and could choose one of two arms. Guillotine style doors separated
88 the entrance chamber from the arms where a large bird cage housing the stooge birds was
89 placed (Figure S2).

90 **Experimental Procedure.** The experimenter held the subject inside the apparatus
91 and showed them each option for six seconds before releasing them into the entrance chamber.
92 Once the subject crossed the threshold of one of the doors, *both* doors were gently closed.
93 After three minutes elapsed, the handler collected the subject and returned them to their
94 home cage. Subjects experience one trial per session per day. **Did we increase this**
95 **toward the end, or was that only numerical?**

96 Each subject experienced five trials (replicate 1) or ten trials (replicate 2) for each of
97 the numerical pairs between 1 and 6 (replicate 1). For replicate 2, we used all numerical
98 pairs between 1 and 6 except those that required more than 8 birds (due to the constraints
99 on the number of stooge conspecifics). The side of the larger option was pseudo-randomized
100 with no left or right runs longer than three consecutive trials. The pairs were organized into
101 blocks with one instance of each pair per block and pairs randomized within each block.
102 **Was this true for food, too?** Subjects ran in a randomized order each day.

Data Analysis

104 All data were analyzed using the same pre-registered analyses (https://aspredicted.org/
105 RVH_MNB) in R version 4.2.1 [38]. To test the first hypothesis, whether pinyon jays prefer
106 larger over smaller numbers of food items and conspecifics, we conducted frequentist and
107 Bayesian one sample t-tests (using the `ttestBF()` function from the *BayesFactor* package
108 with default, noninformative priors [39]).

109 To test our second and third hypotheses, whether numerical difference and ratio
110 predict preferences between smaller and larger options independently, we used generalized
111 linear mixed-effects modeling. We used trial-level choices for either the larger (coded as 1)
112 or smaller (coded as 0) option available in the number pair as the response variable. To
113 investigate our hypotheses, we used model selection to compare which combination of random
114 (subject, pair, or both) and fixed (ratio, difference, or a combination of both) effects best
115 describe each data set (food and social). We draw inferences based on Bayesian statistics
116 (BF values) where a $BF > 3$ is sufficient evidence for the alternative hypothesis, $BF < 1/3$
117 is sufficient evidence for the null hypothesis, and $1/3 < BF < 3$ indicate neither hypothesis
118 has evidence supporting it (suggesting the sample size is too small to draw conclusions).

119 **Results**

120 **Food Experiment**

121   Our first hypothesis predicted that subjects would on average choose the larger number
122 of mealworms over the smaller number across all of the numerical pairs. One sample t-tests
123 provided strong and moderate evidence (respectively) that preferences were above chance
124 (50%) in both replicate 1 ($t(7) = 4.82$, $p = .002$, $\mathrm{BF}_{10} = 24.28$) and replicate 2 ($t(3) = 5.69$,
125 $p = .011$, $\mathrm{BF}_{10} = 6.70$).

126   For both replicates, the best-fitting random effect structure was no random effect
127 structure. Next, the five fixed effect model structures were compared. The model with only
128 the main effect of ratio (Replicate 1: $\mathrm{BF}_{10} = 1.87 \times 10^3$, Replicate 2: $\mathrm{BF}_{10} = 3.79$) best
129 fit both data sets. Thus, subjects in the food experiment used the ratio between the two
130 numbers of mealworms to choose between options, with stronger preferences for larger options
131 at smaller ratios (Figure 1). The model with the main effect of difference had moderate
132 evidence (Replicate 1: $\mathrm{BF}_{10} = 459.68$, Replicate 2: $\mathrm{BF}_{10} = 0.37$) supporting stronger
133 preferences for larger options at larger differences but only for replicate 1. Consequently, this
134 only partially supports our second hypothesis (Figure 1). Additionally, our third hypothesis
135 was not supported, as the interaction model with difference and ratio did not have a $BF > 3$
136 in either replication (see Tables ?? and ?? for full results).

137 **Social Experiment**

138   Hypothesis 1 predicted that subjects would choose the larger number of flock mates
139 over the smaller. One sample t-tests provided moderate evidence that our hypothesis
140 was supported in replicate 1 ($M = 55.33$, 95% CI $[52.34, 58.32]$, $t(9) = 4.03$, $p = .003$,
141 $\mathrm{BF}_{10} = 16.67$). However, evidence supported no difference from chance in replicate 2
142 ($M = 50.19$, 95% CI $[47.06, 53.32]$, $t(9) = 0.13$, $p = .896$, $\mathrm{BF}_{10} = 0.31$).

143   For hypotheses 2 and 3, we again used mixed effect model selection. No random
144 effect structure was used for both replications. For fixed effects, the intercept only model
145 (Replicate 1: $\mathrm{BF}_{10} = 0.07$, Replicate 2: $\mathrm{BF}_{10} = 0.06$) best fit the data, suggesting that
146 neither ratio nor difference influenced choice. Because no model other than the intercept
147 only had evidence suggesting that it was true, neither hypotheses 2 or 3 were supported by
148 the data (Figure 2).

149 **Discussion**

150   We examined pinyon jays' quantitative abilities in choosing between different numbers
151 of food items and social partners. Over all numerical pairs, birds chose the larger of the two
152 options in the food experiment but not in the social experiment, partially confirming our first
153 hypothesis. In the food experiment, smaller numerical ratios predicted the birds' choices but
154 only in the first replicate did larger differences predict birds' choices, partially confirming
155 our second hypothesis. In the social experiment, neither ratio nor difference predicted choice,
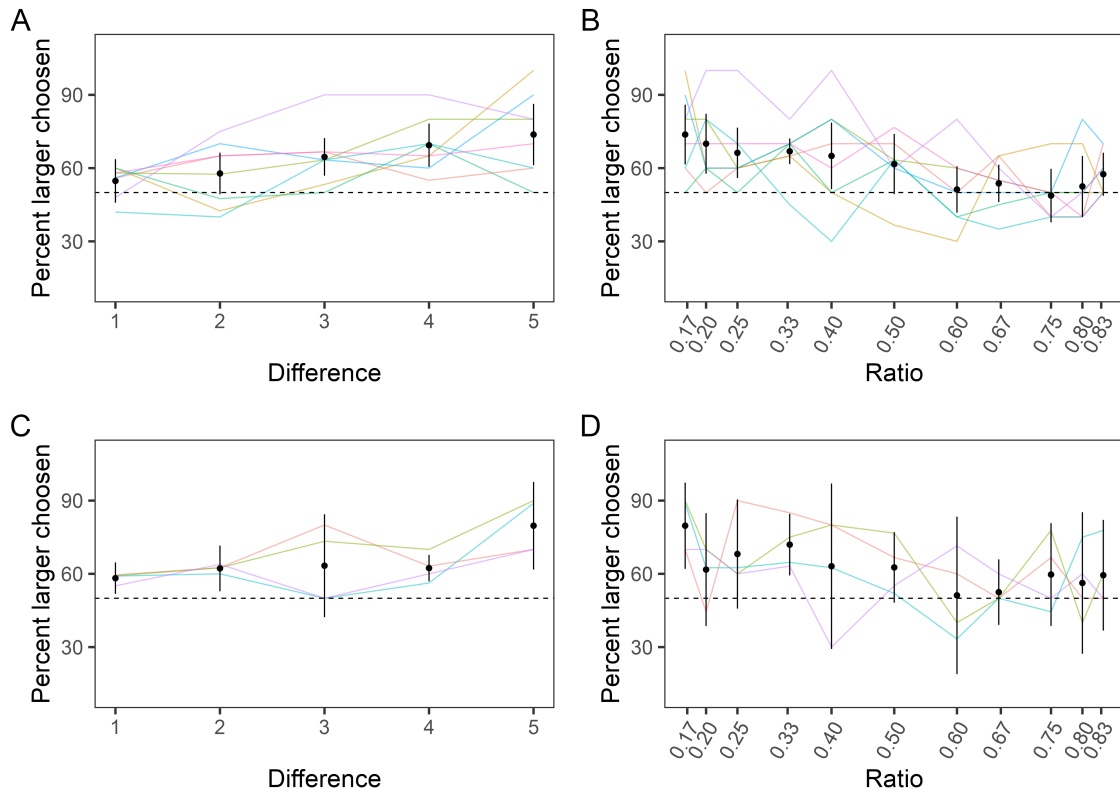
Figure 1. Food experiment difference and ratio results for both replicates. Mean preference for the larger option is shown on the y axis with the numerical difference or ratio options on the x axis. (a) Preference for larger per difference in replicate 1. (b) Preference for larger per ratio in replicate 1. (c) Preference for larger per difference in replicate 2. (d) Preference for larger per ratio in replicate 2. Dots represent mean values across subjects and trials. Error bars represent 95% within-subject confidence intervals. Lines represent individual subject data.

Table 1

Model	AIC	BIC	BF
intercept only	753.54	757.88	1.00
ratio	746.53	755.21	3.79
difference	751.16	759.85	0.37
difference + ratio	747.76	760.79	0.23
difference * ratio	748.62	765.98	0.02
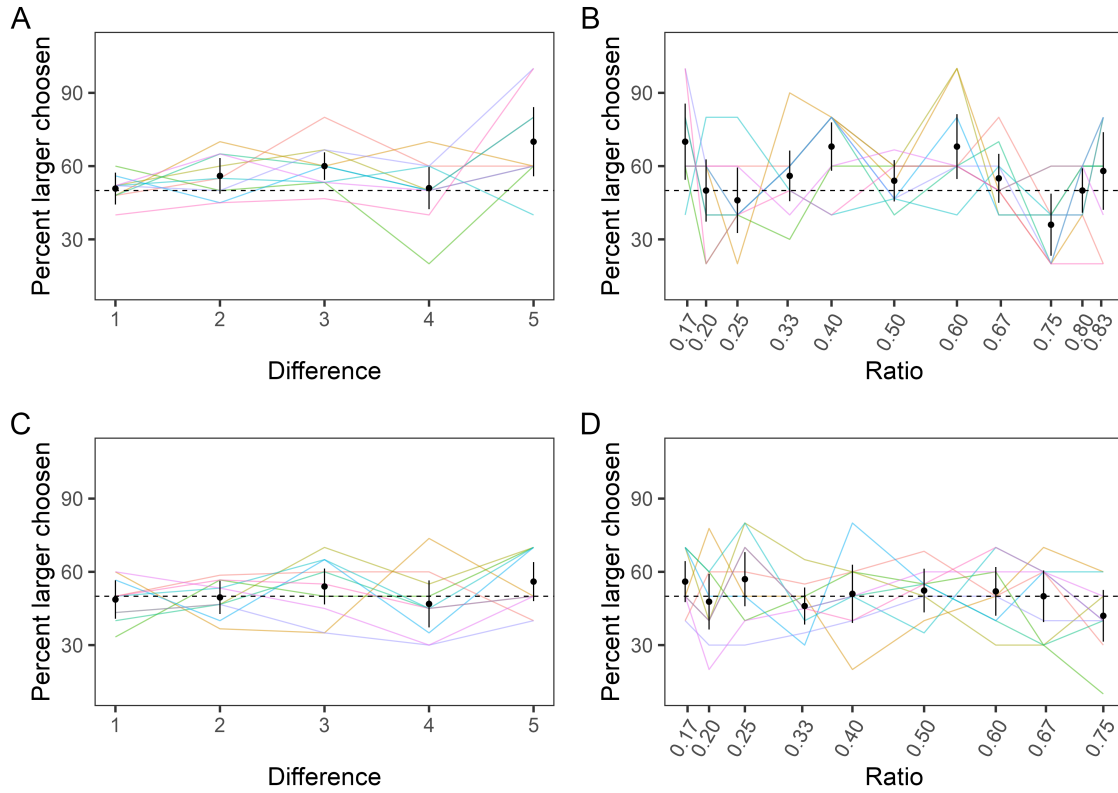
Figure 2. Social experiment difference and ratio results for both replicate 1 and 2. Mean preference for the larger option is shown on the y axis with the numerical difference or ratio options on the x axis. (a) Preference for larger per difference in replicate 1. (b) Preference for larger per ratio in replicate 1. (c) Preference for larger per difference in replicate 2. (d) Preference for larger per ratio in replicate 2. Dots represent mean values across subjects and trials. Error bars represent 95% within-subject confidence intervals. Lines represent individual subject data.

Table 2

Model	AIC	BIC	BF
intercept only	1,609.65	1,614.74	1.00
ratio	1,589.49	1,599.67	1,874.16
difference	1,592.30	1,602.48	459.68
difference + ratio	1,590.90	1,606.17	72.38
difference * ratio	1,592.68	1,613.04	2.34

contradicting our second hypothesis. In both the food and social experiments, difference and ratio did not independently predict choice, contradicting our third hypothesis.

In the food experiment, our pinyon jays preferred larger over smaller quantities more as the numerical ratios decrease, which aligns with previous corvid research demonstrating a numerical magnitude effect [20,24,27]. This provides evidence for pinyon jays using the approximate number system as a mechanism for quantification. However, unlike the previous corvid studies, we did not find conclusive evidence for the numerical distance effect, as number preference did not depend on the difference between two values in either replicate.

In the social experiment, neither ratio nor difference predicted choice, suggesting that pinyon jays do not employ a single mechanism across object types. This outcome is surprising, as previous quantification tasks with conspecifics in fish found effects of difference and ratio [2,3], suggesting that the mechanisms underlying quantification in food and social partners differ. The differences in numerical preference between food and social contexts may be due to different selective pressures. Both foraging techniques and flock size have consequences for evolutionary fitness, but they tackle different adaptive problems. Food consumption acts primarily via natural selection by enhancing survival. Flock size, however, is integral to both natural and sexual selection: natural selection in the form of predator avoidance and sexual selection in the form of mate preference. Joining a larger flock allows an animal to dilute their chances of being eaten by predators (i.e., the dilution effect) but also provides a larger pool of potential mates. For food items and predation risk only number matters but for mate preference or other social preferences, the identity of the partners matters. One possible explanation for the lack of a ratio or difference effect for the social preference task is that individual identity of birds overrides the importance of number. An exploratory follow-up analysis of our data showed wide variation in preferences for groups that contained individual stooge birds (Table S?). Pinyon jays have complex, long-term bonds with other flock members and mates [40], which may make identity of group mates more important than sheer numbers. Moreover, the birds in our studies did not experience signals of predation danger during the experiment. Without pressure to dilute risk in larger groups, the birds may have ignored group size, allowing them to use other information such as social partner identity to determine choice.

Our study design does not allow us to pinpoint the exact features by which the birds make these quantitative choices. For the food preference tasks, the birds may choose larger *numbers* of food items or larger *amounts* of them. Using number involves tracking the quantity of individuated objects. However, in many cases, animals choose based on amount, which refers to other measures or proxies of quantity such as item size, surface area, volume, perimeter, and density [5,41,42,**Menzel.1960?**]. **Menzel, E. W. (1960). Selection of food by size in the chimpanzee, and comparison with human judgments. Science, 131, 1527–1528. https://doi.org/10.1126/science.131.3412.1527** It is possible that our jays used, for example, surface area to choose their food items. This is a reasonable criteria because surface area may be a better proxy of total calories than absolute number. Future work is needed to tease apart which features birds use to make quantitative decisions.

Conclusion

This research investigated how pinyon jays assess numbers of food items and conspecifics in preference tasks. For food items, numerical ratio predicted their choices in both replicates while numerical difference predicted choice in only the first replicate, but neither ratio nor difference predicted choices in the social experiment. Though quantity is important for selecting food items, other factors such as flock mate identity may be more important for selecting social groups to join. Thus, in quantification situations, the type of objects to be quantified may drive the cognitive processes that animals use. Furthermore, many adaptive problems beyond foraging require sensitivity to quantities, and we encourage further exploration of numerical cognition of non-food objects.

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Ethics approval

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