

Rosy-faced lovebirds are capable of associative symbol learning and inference-based quantity discrimination

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Cognitive capacity for associative learning and quantity discrimination is highly adaptive in various ecological contexts and subject to convergent evolution across diverse animal species. Discrimination accuracy generally increases with the ratio between two quantities in many studied animals; however, this ability is expected to vary among species, highlighting the need to understand how it operates in different taxa. Parrots are among the most intelligent birds, but only a few parrot species have been studied for their associative learning and quantity discrimination abilities. To investigate these cognitive capabilities in small parrots, we presented a novel symbol system to 28 rosy-faced lovebirds, *Agapornis roseicollis*. This system associates additive tally marks with symbols representing a one-to-one correspondence with different food quantities. We specifically tested three aspects of cognition related to numerical competence, namely associative learning, inference and quantity discrimination. Trained lovebirds could spontaneously infer the relative food quantities represented by other symbols. Lovebirds proved capable of (1) associating symbols (i.e. object-file symbolism) with (2) 'more-less' quantity inference by deducing food quantities based on their knowledge of this symbol-quantity association and (3) enhancing their performance in relation to disparity ratio (conforming to Weber's law) and absolute difference. Furthermore, (4) the influence of food ratios and absolute differences varied with different ratio ranges. Within a small ratio range (≤ 3), increasing the ratio or absolute difference enhanced discrimination performance. However, within a higher ratio range (> 3), these characteristics had less of an impact. We concluded that rosy-faced lovebirds are capable of advanced associative learning and quantity discrimination, similar to larger parrot species.

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The ability of animals to discriminate quantities in the contexts of resource acquisition, competition and risk aversion is a highly adaptive facet of cognition, conserved under strong selection pressures (Bryer et al., 2021; Nieder, 2020b). Quantity discrimination is thus ubiquitous across taxa, exemplified among mammals (primates [Beran et al., 2015], cetaceans [Abramson et al., 2013], carnivores [Baker et al., 2012; Pisa & Agrillo, 2009], ungulates [Caicoya et al., 2021] and rodents [Reznikova et al., 2019]), birds (Garland et al., 2012), reptiles (lizards [Szabo et al., 2021] and archosaurs [Gazzola et al., 2018]), amphibians (Krusche et al.,

2010), bony fish (Agrillo et al., 2008), sharks (Brown & Schluessel, 2023), and even invertebrates (Bisazza & Gatto, 2021; Gatto et al., 2022). Judging quantities can be advantageous in multiple life contexts, including optimal foraging (Arehart et al., 2023; Cresswell & Quinn, 2004; Gatto et al., 2022), conspecific communication and cooperation (Salena & Balshine, 2020; Templeton et al., 2005), assessing numerical advantage in inter-group conflicts (Benson-Amram et al., 2011; Buesching & Jordan, 2019, 2022; Rivas-Blanco et al., 2020), avian egg counting (Garland et al., 2012; Tornick et al., 2015) and brood parasite avoidance (Garland et al., 2012; Lyon, 2003), group affiliation (Xiong et al., 2018) and distinguishing sex ratio in mating (Flay et al., 2009; Hardy, 2002) and local resource competition (Cockburn et al., 2002) contexts, inter alia. These quantitative

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assessments also often interact with qualitative perceptual cues; for example, black-capped chickadees, *Poecile atricapilla*, encode information about both predator number and size in their alarm calls (Templeton et al., 2005). Furthermore, quantitative discrimination is mediated by social factors, such as flock behaviour and dominance (Kelly, 2016). It is also influenced by whether the ability being tested is spontaneous (that is, the innate capacity to choose between quantities of biologically relevant stimuli) or trained (that is, learnt discrimination by selecting a larger set of neutral stimuli to receive a reward; Petrazzini et al., 2018). Consequently, it has proven challenging to derive a comprehensive and systematic understanding of the cognitive mechanisms underlying quantity discrimination, particularly given the diverse contexts, species and environments that shape this ability (Bryer et al., 2021).

To address this complexity, different theories have been proposed to explain specific forms of quantity discrimination (Addessi et al., 2008; Baker et al., 2012; Bogale et al., 2011). The analogue magnitude mechanism has been established as a key framework for representing and comparing quantities in diverse animals (Addessi et al., 2008; Baker et al., 2012; Bogale et al., 2011). The analogue magnitude mechanism involves the attribution of an analogue representation proportional to the objects' properties (e.g. number, size, length or surface). Such an analogue representation has no limit, which allows the depiction of large numbers (Feigenson et al., 2002). Within such a mechanism, the ability of animals to perform quantity discrimination tends to conform to Weber's law (Rivas-Blanco et al., 2020), a psychological concept that describes how the perception of a difference in a stimulus depends on the original intensity of the stimulus (Pardo-Vazquez et al., 2019). The capacity to discriminate between two quantities thus typically increases as the ratio between the larger and smaller number increases (that is, animals should perform better when discriminating between eight and one items, a ratio of eight, than between eight and four items, a ratio of two; Agrillo & Bisazza, 2014). Quantity discrimination is further affected by the magnitude (defined as the total amount across both quantities, for example, the magnitude of eight versus four would be 12) and the disparity (that is, the absolute difference between the two quantities; for example the disparity of eight versus four would be four) of differences between contrasted quantities. Consequently, performance decreases as magnitude increases, disparity decreases, and as the ratio between contrasted quantities becomes more even (Irie & Hasegawa, 2012). Such ratio-based quantity discrimination has been found across vertebrate (Nieder, 2020a) and invertebrate species (Gatto et al., 2022). Nevertheless, research examining quantity discrimination patterns within identical magnitudes, that is, exploring whether the absolute difference between two quantities (rather than their ratio) is decisive in animal choice, remains scarce.

The use of inferential reasoning as a process for making judgement calls based on available evidence allows animals to apply prior knowledge to decision-making in novel scenarios (Premack, 1995; Vigo & Allen, 2009). Specifically, transitive inference is a form of deductive reasoning that allows a relation between items that have not been explicitly compared before to be derived (Vasconcelos, 2008). Thus, in a general form, transitive inference is the ability to deduce that if item A is related to item B and item B is related to item C, then item A must be related to item C. Such inferential reasoning has been established in various mammal species (Völter & Call, 2017), especially in primates (MacLean et al., 2008), but is also a feature of the advanced cognitive abilities of certain bird taxa (Bond et al., 2010; Mikolasch et al., 2013; Pepperberg, 2006). Furthermore, African grey parrots, *Psittacus erithacus* (Clements et al., 2018), and kea, *Nestor notabilis*

(Bastos & Taylor, 2020), are capable of probabilistic reasoning, inferring a sample based on prior knowledge about a population.

Parrots (Psittacidae) and corvids (Corvidae) have been termed 'feathered apes' (Emery, 2004; Lambert et al., 2019) in the literature due to their exceptional cognitive capacities, which are comparable to those observed in primates (Güntürkün et al., 2017). Testing of quantity discrimination in African grey parrots (Ain et al., 2009) and Eurasian jackdaws, *Coloeus monedula* (Ujfalussy et al., 2014) has shown that performance improves with larger ratios. Jungle crows, or large-billed crows, *Corvus macrorhynchos*, can even be trained to learn that a five-circle symbol on a cup indicates a reward inside, while a two-circle symbol does not (Bogale et al., 2011). Moreover, in a task with five quantity combinations (three versus five, four versus five, five versus six, five versus seven, five versus eight), jungle crows attained higher accuracy with higher ratios (Bogale et al., 2011). It is thus reasonable to anticipate that parrots and corvids may be able to solve a 'more-less' paradigm by inference from symbols representing specific food quantities; that is, associative symbol learning (Hummel, 2010). Nevertheless, despite emerging interest in parrot cognition, comprehensive and detailed studies have primarily focused on a limited number of large Psittacidae species (Auersperg & Bayern, 2019). It remains largely unexplored whether other, especially smaller, parrot species show comparable cognitive performance, including numerical competence.

Rosy-faced lovebirds, *Agapornis roseicollis*, are highly social, small-sized parrots native to arid regions in southwestern Africa (Huynh et al., 2023), where food resources vary substantially across seasons (Ndithia & Perrin, 2006b). Here, they forage socially on a highly selective diet (Ndithia & Perrin, 2006a). Since coping with environmental and social challenges is expected to promote cognitive abilities (Social Intelligence Hypothesis: Humphrey, 1976; Jolly, 1966; Social Brain Hypothesis: Dunbar, 1998; Cultural Intelligence Hypothesis: Whiten & van Schaik, 2007), rosy-faced lovebirds are well suited for testing predictions regarding cognitive abilities related to numerical competence. In addition, their popularity as companion pets (Chan et al., 2021) makes them readily accessible for behavioural studies, which facilitates data collection with a relatively large sample size. We thus used rosy-faced lovebirds as a model to test three predictions. First, we asked whether rosy-faced lovebirds are capable of associative learning, specifically object-file symbolism. We predicted that individuals would preferentially choose feeders marked with symbols indicating the presence of food or greater quantities over those marked with symbols representing no food or smaller quantities, respectively, following training. Second, we asked whether they are capable of 'more or less' quantity inference. We predicted that, after learning symbol-quantity associations, they would be able to deduce food amounts based on prior knowledge of symbol-quantity association and prefer feeders associated with greater food rewards. Third, we investigated whether the birds' discriminative ability improves with increasing disparity ratio, in line with Weber's law, and absolute difference. We predicted that individuals could better distinguish between quantities when the numerical ratio and absolute difference between them were larger.

METHODS

Study Animals and Housing Conditions

Experiments were conducted using 28 adult rosy-faced lovebirds (19 males and 9 females, aged 2 to 4.5 years old; Table S1) housed individually in wire-mesh cages (60 × 40 × 40 cm) under a 12:12 h light:dark cycle (6500K illumination; LED T5 tube, 7W, SUNSHINE) at the Centre for Comparative Medicine Research

(CCMR) animal facility at the University of Hong Kong. The ambient temperature was kept at 22 °C–24 °C and the humidity between 50% and 60%. Artificial food pellets (Mazuri Small Bird Maintenance Diet 56A6) and UV-filtered water were available *ad libitum* and changed daily.

Ethical Note

All procedures were approved by the Committee on the Use of Live Animals in Teaching and Research (CULATR; approval number: 5883–21) and under a Department of Health Animal (Control of Experiments) Ordinance Chapter 340 permit ([21–1146] in DH/HT&A/8/2/3 Pt.32). Birds were housed individually in separate cages to prevent aggressive behaviour stemming from their territorial nature and aggression. To ensure their well-being, we provided them with environmental enrichment, such as toys, chewing materials and music. The same classical music was played for all birds throughout the study, with no variation in auditory stimuli between individuals. The cages were arranged in one room, allowing the birds to maintain visual and auditory contact with

each other. The birds were obtained from local breeders and were involved in other projects after this study.

Experimental Protocol

The same experimental setup was used to first investigate associative symbol learning and inference, and then symbol-indicated quantity discrimination ability. Each bird was tested individually in its cage by providing a perch (length = 30 cm) with a stainless steel cylindrical cup (diameter × height: 5 × 5 cm) attached to each end (Fig. 1a). A camera (STARCAM CB71–C / STARCAM CB73 Mini Battery IP Camera) was placed on top of the cage to record bird behaviour. Birds were able to move freely around the cage and access both cups equally from the perch. These cups were covered with tightly fitted white paper lids (diameter: 7 cm, weight/area: 2.3 g/100 cm²), upon which symbols were printed using red food-grade dye. In addition, laminated vertical signs with identical corresponding symbols were affixed behind each cup (Fig. 1a). We used a circle (that is, 'O', 23 mm in external diameter and 17 mm in internal diameter; hereafter

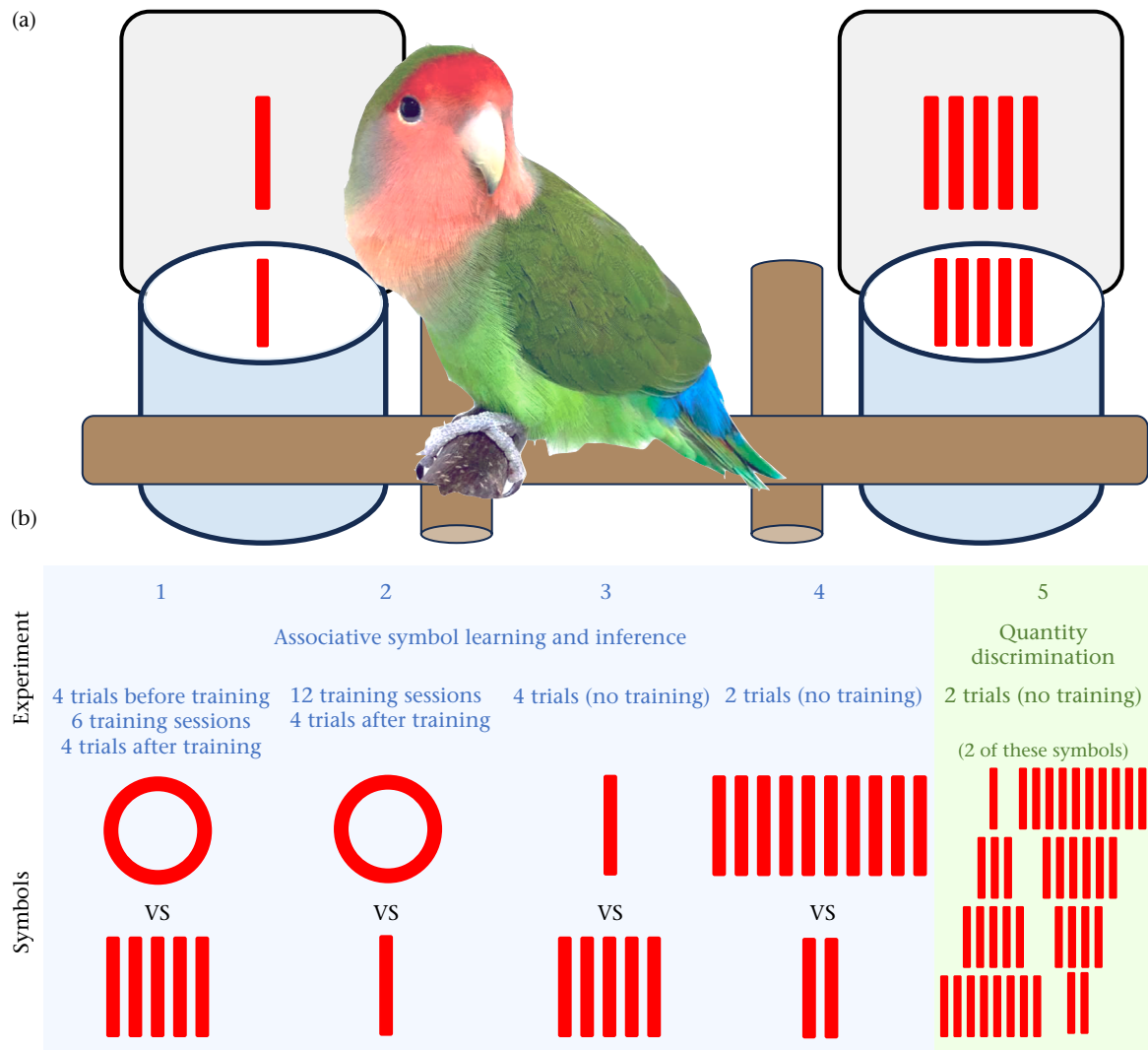


Figure 1. Schematic overview of the experimental design. (a) Experimental protocol. Food rewards were hidden in stainless steel cups during trials. Symbols were shown on and behind the cups. (b) The five experiments conducted on associative symbol learning, inference and quantity discrimination, and the symbol combinations used. Experiment 1: zero versus five, four trials before training + 6 training sessions + 4 trials after training. Experiment 2: zero versus one, 12 training sessions + 4 trials after training. Experiment 3: one versus five, four trials (no training). Experiment 4: two versus 10, four trials (no training). Experiment 5: two trials for each combination of symbols (see Table 1).

referred to as 0) to indicate an empty cup and different numbers of bars (that is, '|', measuring 23 mm in length and 3 mm in width, separated by a gap of 2 mm) to indicate specific food reward portions concealed under the white paper lid in each respective cup (Fig. 1b). For instance, one bar (i.e. '|') indicated one sunflower seed and one food pellet in the cup, whereas two bars '||' indicated two sunflower seeds and two food pellets in the cup, etc. For clarity, we use Arabic numbering system hereafter to represent all symbols in the text.

We limited the number of trials to one per bird per day to minimize the effects of satiation. To motivate birds to participate in the discrimination trials, we closed their feeders for 1.5 h before the start of each trial as well as for 20 min after the conclusion of the experiment. This fasting procedure has encouraged lovebirds to participate during trials in a previous study (Tsang et al., 2024). We then simultaneously attached both experimental feeder cups to the perch in the subject parrot's cage and gave the bird 10 min to tear the paper lid off the cup(s) and consume the food therein, after which both cups were removed. We defined a choice as occurring when the bird tore the paper off a cup and visually inspected the food inside. None of these birds had previously participated in any symbol-discrimination tests. We then conducted a sequential series of experiments to examine the ability of lovebirds in associative symbol learning, inference and the discrimination of quantities.

Associative Object Symbol Learning and Inference

Before commencing these associative learning trials, we first established whether lovebirds had any intrinsic preference for a particular symbol. For this, we conducted four trials presenting cups with 0 against cups with five, controlling for left–right side bias and potential morning–afternoon differences (that is, the position of each cup/symbol was switched in the two trials in the morning, 1100–1200 hours, and in the two trials in the afternoon, 1600–1700 hours).

We then trained the birds to associate the symbol 0 with the absence of food and the symbol five with the presence of abundant food to test the ability of lovebirds to form an association between specific symbols indicating the presence (in one cup) or absence (in the other cup) of food (that is, inference by exclusion through object-file association). During this training period, we removed approximately one-sixth of the paper lid area without damaging the printed symbols, allowing lovebirds to see the content inside the food cup and make informed choices. Nevertheless, lovebirds still needed to exert effort to tear the paper lid away to fully access the food. Six rounds of training were conducted for this zero versus five symbol combination, and the symbols were provided three times in each position (that is, left or right) in random order for each bird, but avoiding the same position for three consecutive trials.

After the training sessions, we conducted four experimental trials to test whether the lovebirds had learnt to associate symbols with the presence or absence of food (Fig. 1b, experiment 1). We presented zero versus five (Video S1), with cups fully covered with paper lids bearing corresponding symbols. During pretraining trials, the four trials were controlled for left–right side bias and potential morning–afternoon differences.

We then implemented a similar training protocol as above for the symbol combination zero versus one (Video S2), followed by four experimental trials for zero versus one (Fig. 1b, experiment 2; Video S3). Twelve rounds of training were conducted for this zero versus one symbol combination, due to the low interest birds had in small food rewards, with the symbols provided six times in each position (i.e. left or right).

After the zero-versus-one trials, we performed a second experiment to test whether the lovebirds had learnt to associate the different symbols (one versus five) with different quantities of food. For this task, we conducted four trials of one versus five without providing any additional training (Fig. 1b, experiment 3).

We subsequently tested whether lovebirds could infer relative food quantities from additive bars comprising new symbols, based on the symbols they had learnt during the associative learning. In two experimental trials, we presented combinations of two new compound symbols (i.e. two versus 10), where the number of bars in each symbol was double that of the previously learnt symbols (i.e. one and five), while adhering to the same ratio disparity (Fig. 1b, experiment 4). This experiment was conducted during the morning session only to exclude performance differences between the morning and afternoon sessions.

Quantity Discrimination

To investigate what mechanism lovebirds use to discriminate quantities, ratio disparities or absolute amounts, we provided food quantity combinations at disparity ratios of 1.25, 2, 3, 4, 5, 8 and 10, as well as two combinations with different absolute differences in each of the ratios 2, 3, 4 and 5 (Table 1, Fig. 1b). We ran two trials for each symbol combination, with different left–right positions to control for potential side bias. The symbol position in each combination was randomized in the first trial. All trials were carried out in the morning. The use of the same symbol in two consecutive combinations and any combination consisting of a familiar symbol alongside a symbol with a novel number of bars was avoided. In ca. 1% of all trials, the bird did not participate (that is, showed no interest in either feeder). In these cases, we repeated the trial only once, and the trial was recorded as a missing value if the bird also did not participate in this second reiteration.

Statistical Analyses

Analyses and associated illustrations were performed and generated using RStudio (Version 4.2.2; R Core Team, 2022). We ran generalized linear mixed models with binomial distribution using the R package lme4 v1.1-31 (Bates et al., 2015) to examine the influence of symbol position (left/right) on the feeder cup (left/right) chosen by birds in each combination, including bird ID and trial ID as random effects, that is, model 1 choice position ~ symbol position + (1|ID) + (1|trial). We then ran beta regression models using the R package betareg v3.1-4 (Cribari-Neto & Zeileis, 2010) to investigate the effects of food quantity ratio and absolute difference on the proportion of trials in which a bird selected the most rewarding feeder cup as its first choice: model 2 the proportion of first choices selecting the greater food reward ~ absolute difference × ratio; model 3 the proportion of first choices

Table 1
Symbol combinations tested for quantity discrimination

Absolute difference	Ratio						
	1:1.25	1:2	1:3	1:4	1:5	1:8	1:10
9							1 vs 10
8					2 vs 10		
7						1 vs 8	
6				2 vs 8			
5							
4		4 vs 8	2 vs 6		1 vs 5		
3				1 vs 4			
2			1 vs 3				
1	4 vs 5	1 vs 2					

selecting the greater food reward ~ ratio $\times$ ratio level ('low' when ratio ≤ 3 , 'high' when ratio > 3). The ratio cutoff of 3 was chosen based on the animals' divergent behavioural patterns between ratios ≤ 3 and > 3 (see Results for details); and model 4, the proportion of first choices selecting the greater food reward ~ absolute difference $\times$ ratio level. We initially included symbol familiarity, defined as the number of times each symbol had been seen before testing a symbol combination, and test order, i.e. the sequence of symbol combinations tested, as predictors in models 2 to 4 to evaluate their possible impact on the proportion of first choices that selected the greater food reward. However, these variables were not statistically significant ($P > 0.05$) and did not improve model fit based on Akaike Information Criterion (AIC) and the Bayesian Information Criterion (BIC) comparisons. For all models, the versions excluding these predictors had lower AIC and BIC values: model 2 ($\Delta\text{AIC} = 3.094$, $\Delta\text{BIC} = 3.890$), model 3 ($\Delta\text{AIC} = 2.732$, $\Delta\text{BIC} = 3.528$) and model 4 ($\Delta\text{AIC} = 0.918$, $\Delta\text{BIC} = 1.714$). Consequently, they were excluded from the final models.

We evaluated the performance of each lovebird in the quantity discrimination test (Table 1), where each symbol combination was presented in two trials. We used the Kruskal–Wallis test (package 'stats' in base R) to assess individual performance differences across symbol combinations: Model 5) individual proportion of first choices selecting the greater food reward in each symbol combination ~ individual ID. A beta regression model (Cribari-Neto & Zeileis, 2010) was used to investigate any association between an individual's performance and their sex, age and weight: Model 6) individual proportion of first choices selecting the greater food reward across all symbol combinations ~ sex, age and weight. The objectives and types for each model were summarized in Table S2. Additionally, we conducted a correlation test to evaluate whether an individual's overall tendency to choose the greater food reward across all symbol combinations was associated with their preference for the greater reward symbol in low-ratio combinations (ratio ≤ 3). All assumptions of the statistical models were assessed and met (Table S2).

RESULTS

Associative Symbol Learning and Inference

Before the lovebirds were trained with the zero versus five cup/symbol combinations, the placement of the symbols did not influence which food cup they picked, as they chose either symbol almost equally (symbol five was chosen 49.53% of the time; model 1: $P = 0.885$; Table 2, Fig. 2). After training, however, the proportion of first choices selecting the symbol indicating the food reward cup increased to 71.17% (model 1: $P < 0.001$; Table 2, Fig. 2). After training with zero versus one symbol combinations, lovebirds picked the cup marked with the food reward symbol 60.55% of the time, which was significantly more than the empty symbol

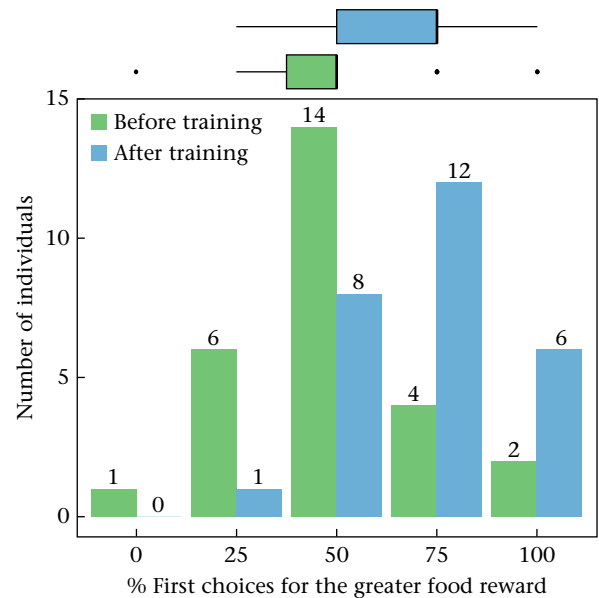


Figure 2. Performance changes before and after zero versus five associative symbol training. The vertical bars represent the number of individuals at different proportions of their first choice for the greater food reward, before and after training. The horizontal box plot summarizes the distribution of the individuals across the proportion of first choice for the greater food reward before and after the training.

(model 1: $P = 0.012$; Table 2), but this amount was less than their choices in the zero versus five trials (Table 2). In the one-versus-five trials, even without any prior training, lovebirds selected the symbol indicating the greater food reward significantly more often (65.18%) than the symbol indicating the cup containing less food (model 1: $P = 0.001$; Table 2).

When lovebirds were presented with the new symbol combination of two versus 10, they were significantly more likely to choose the symbol indicating the greater food reward, that is, symbol 10 (67.86%) rather than symbol two (model 1: $P = 0.019$; Table 2).

Quantity Discrimination

There was a clear tendency for lovebirds to choose symbols indicating the greater food quantity over symbols indicating the lesser food quantity (Table S3, Fig. 3). This scenario was the case for all symbol combinations tested except four versus five. For all combinations with ratios > 3 , lovebirds chose symbols indicating a greater quantity of food significantly more often than the symbol indicating a lesser quantity of food (Table S3, Fig. 3).

The proportion of choices for the symbol indicating a greater quantity of food was associated with the ratio of two quantities (model 2: $P < 0.001$; Table S4), absolute difference (model 2: $P <$

Table 2
Performance in associative symbol learning and inference

Combinations	Proportion of first choices for the greater food reward (%)	Estimate	P
0 vs 5 before training	49.53	−0.067	0.885
0 vs 5 after training	71.17	2.249	< 0.001***
0 vs 1 after training	60.55	1.331	0.012*
1 vs 5	65.18	1.537	0.001**
2 vs 10	67.86	1.708	0.019*

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

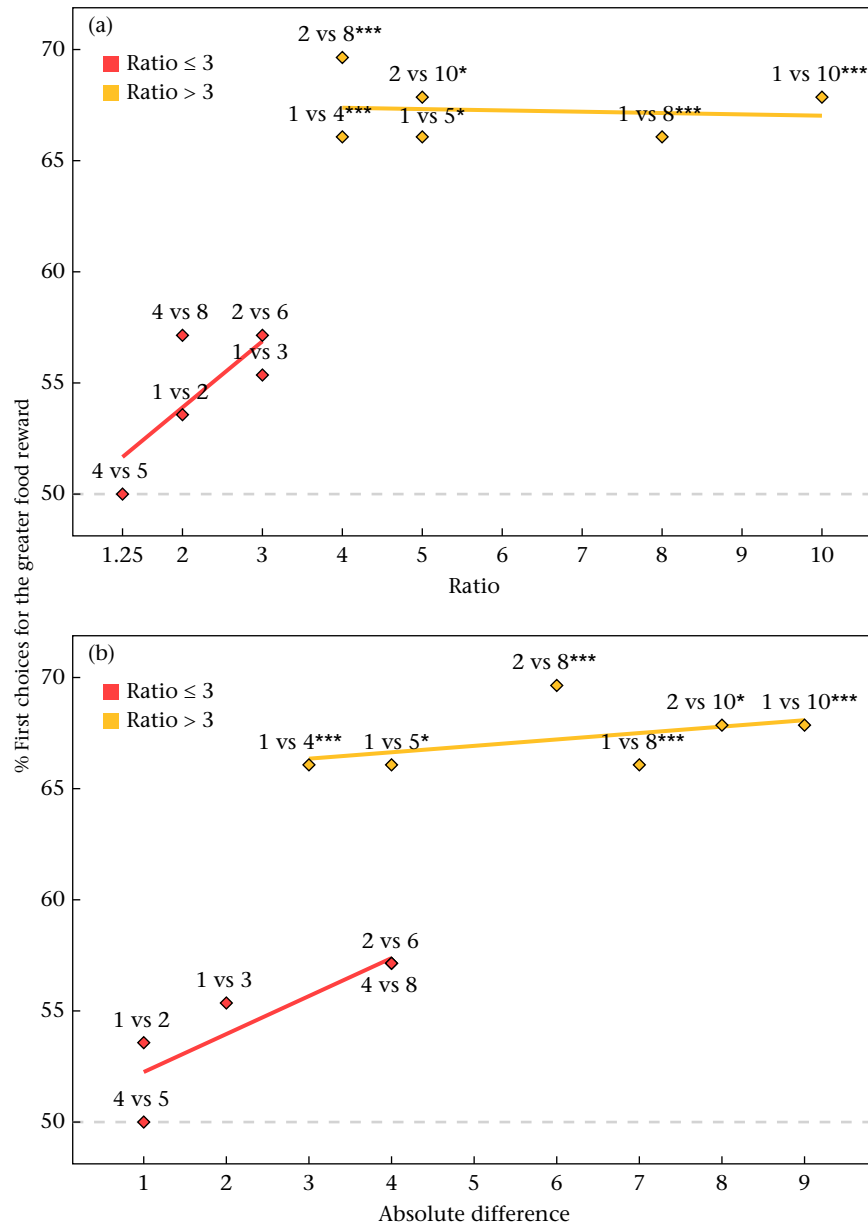


Figure 3. The proportion of lovebirds that first opened the cup with the greater food reward as a function of (a) the ratio or (b) the absolute difference indicated between the two symbols. The two fitted lines refer to two ratio levels. Significant results are marked with asterisks: * indicates $P < 0.05$; ** indicates $P < 0.01$; *** indicates $P < 0.001$.

0.001) and their interaction (model 2: $P < 0.001$). The proportion increased among combinations with higher ratios when ratios were low (between one and three), rising from 50% to 58%, and increased more substantially between ratios of three and four. However, the proportion became stable at high ratios (>3), with a preference range of 66%–70% for the higher food reward symbol (Fig. 3a). A ratio of 3 (i.e. a ratio ≤ 3 versus >3) was the general threshold of lovebird discrimination ability (model 3: $P = 0.006$; Table S4). Similarly, absolute differences in food quantities also showed an effect on the proportion of instances in which lovebirds chose the symbol indicating the greater quantity of food. The influence of absolute differences in food quantities on symbol selection also differed between different ratio ranges (ratio ≤ 3 versus >3 ; model 4: $P = 0.006$; Table S4, Fig. 3b): at ratios ≤ 3 , the choice for the symbol indicating a greater quantity of food increased noticeably with absolute differences in food quantity; at ratios >3 , this increase was shallower. Within the same ratio band,

lovebirds showed a tendency to choose the symbol indicating the greater quantity of food more often for combinations with larger absolute differences than for those with smaller absolute differences (Fig. S1).

Interindividual Variation in Quantity Discrimination

We detected significant individual performance differences across symbol combinations (model 5: $\chi^2(27) = 41.434$, $P = 0.037$; Table S4). Individuals with the highest tendency to select the greater food reward symbol as their first choice also tended to show the highest tendency to select the greater food reward symbol at low-ratio combinations ($r = 0.276$, $P < 0.001$; Fig. 4). Sex (model 6: $P = 0.231$; Table S4), age (model 6: $P = 0.707$) and body weight (model 6: $P = 0.883$) showed no association with an individual's quantity discrimination performance.

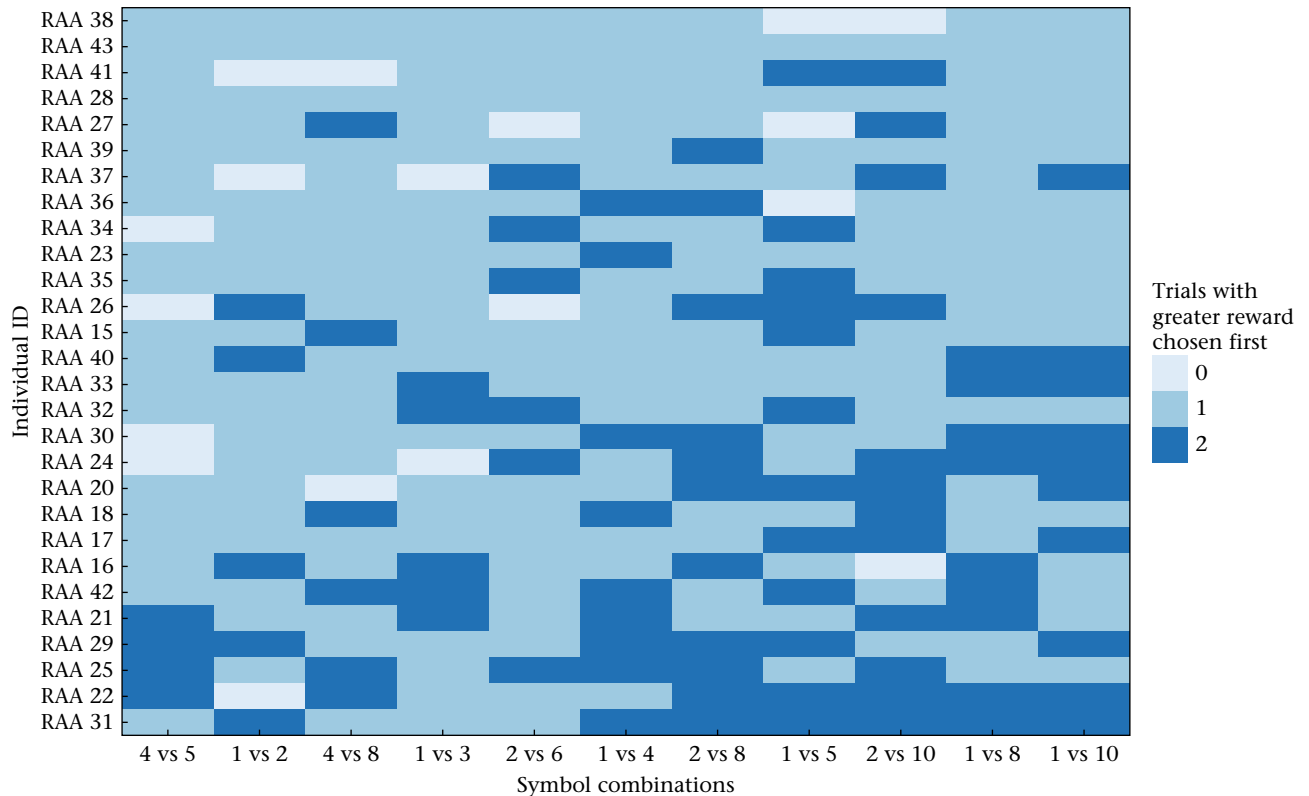


Figure 4. Individual differences in the number of trials where the greater food reward was chosen first, across all symbol combinations in the quantity discrimination test (2 trials per combination). Individuals are ordered according to their overall proportion of first choices for the greater food reward in all combinations, with the individuals with the highest proportion located at the bottom. Symbol combinations are ordered by their ratio, with the lowest displayed on the left.

DISCUSSION

Our three principal predictions relating to associative learning and inference ability in rosy-faced lovebirds were well supported, with birds proving capable of (1) associating symbols (i.e. object-file symbolism) with (2) 'more-less' quantity inference by deducing food quantities based on their knowledge of this symbol-quantity association and (3) enhancing their performance in relation to increasing disparity ratio (conforming to Weber's law) and absolute difference.

Associative Learning of Symbol-quantities

Rosy-faced lovebirds were quickly trained to associate a specific food quantity with a 'I' symbol(s) and distinguish this from an 'O' symbol, indicating an empty feeder. This rapid associative learning is a trait they share with various other psittaciform species, including red-shouldered macaws, *Diopsittaca nobilis*, and black-headed parrots, *Pionites melanocephala* (van Horik & Emery, 2018), as well as species from other avian taxa, including jungle crows (Bogale et al., 2011) and New Zealand robins, *Petroica longipes* (Shaw et al., 2015). One highly trained African grey parrot, named Alex, could even understand the quantities represented by Arabic numbers (Pepperberg, 2006). In contrast, common pigeons, *Columba livia*, are slow learners, but after 3720 training sessions still proved capable of linking precise numerosities with their corresponding symbols (Xia et al., 2001). This difference in counting-related associative learning task performance between avian species likely reflects interspecific cognitive biases (Emmerton, 2001).

'More-less' Quantity Inference

Lovebirds were not merely capable of learning to associate symbols with food presence-absence; our result suggests that they could also comprehend the meaning of a food-indicating symbol representing a greater quantity of food, enabling them to infer when the symbol combination on one feeder lid indicated the presence of a greater food reward than that on the other feeder lid. This was observed even when they were presented symbols that had never been presented together before (i.e. one versus five), indicating the cognitive ability of transitive inference. The capacity to comprehend symbolic representations of quantity is an ability lovebirds share with African grey parrots (e.g. Alex; Pepperberg, 2006), but also with common pigeons, which can be trained to peck a certain number of times (one, two, three or four pecks) on a key that displayed one of several possible numerical symbols (Xia et al., 2000). Similarly, jungle crows can be trained using circle symbols to understand the more-less concept and extrapolate to novel quantity comparisons (Bogale et al., 2011).

Rosy-faced lovebirds could further infer and extrapolate the food quantities indicated by novel symbol tallies, indicating a capacity for ordinality, an ability shared with rufous hummingbirds, *Selasphorus rufus* (Vámos et al., 2020). Lovebirds chose the feeder symbolized with 10 over the feeder symbolized with two in an equal proportion of five versus one. They have learnt that a great number of bars in scenario A indicates greater food rewards and generalized that to choose a great number of bars in scenario B when the number of bars has been doubled. This behaviour displays a form of inductive inference, where an extrapolation is made based on previous learning, as this relates to increasing quantities while preserving the same ratio (Lazareva et al., 2001).

Such ability has also been observed in trained primates, squirrel monkeys, *Saimiri sciureus* (Olthof et al., 1997), and rhesus monkeys, *Macaca mulatta* (Brannon & Terrace, 1998). Pepperberg's (2006) work with Alex the grey parrot similarly found that it could infer the relationship between an Arabic number and a corresponding quantity. This was achieved through stimulus equivalence, a cognitive process where an individual recognizes that different stimuli represent the same underlying concept. Additionally, Alex understood the ordinal relationship among these numbers. However, the possibility that the observation in lovebirds was due to associative learning without inference involved cannot be excluded.

Quantity Discrimination: More Than Just Ratio

Our results support an analogue magnitude mechanism (Carey, 2001); that is, as the ratio between feeder pairs increased, the proportion of choices for the feeder containing the greater quantity of food also increased (Fig. 3a). This study shows that lovebirds' decisions were affected by both the numerical ratio and the stimuli magnitude. This conclusion conforms with Weber's law, which states that the ability to discriminate between two quantities depends on their ratio rather than their absolute difference (Ain et al., 2009; Uller et al., 2003; Uller & Lewis, 2009). Such ratio-dependent discrimination follows a Weber-fraction signature, meaning that the 'just noticeable difference' between pairs of numerosity increases proportionally with the numerical magnitudes (Ditz & Nieder, 2016).

This ability of quantity discrimination has been widely noted across the animal kingdom (Lorenzi et al., 2021), from vertebrates to invertebrates (Ain et al., 2009; Beran et al., 2013; Carazo et al., 2009; Gatto et al., 2022; Gómez-Laplaza & Gerlai, 2011; Lin et al., 2021; Lucon-Xiccato et al., 2018). The analogue magnitude system enables individuals to make rapid comparisons without quantity limits (Dehaene, 2009) and enables both continuous and discrete amounts to be compared (Ain et al., 2009). In our experiment, lovebirds could not directly observe quantities or volumes and form an object-file representation on that basis (e.g. Feigenson et al., 2002); rather, they learnt to associate a bar with a specific food quantity as a one-to-one correspondence between object files.

In addition to analogue magnitude effects, we observed that an absolute difference between feeder pairs promoted the rate at which lovebirds chose the more rewarding feeder (Fig. 3; Fig. S1), which has also been observed in African grey parrots (Ain et al., 2009). Many studies overlook this effect or consider it inconsequential (Nieder, 2020a; but see Bortot et al., 2019; Tan, 2010). However, Nieder (2020a) has shown that not every vertebrate species he tested for numerical cognition could flexibly discriminate absolute numerosity, suggesting that qualitative differences in numerical intelligence exist among vertebrates.

Furthermore, our modelling revealed a modest but significant interaction term between feeder quantity ratio and absolute difference (model 2; Table S4), such that the impact of absolute differences weakens at higher ratios, which suggests that the role of absolute quantity is secondary. With large ratio disparities, the pronounced magnitude of difference between quantities likely overwhelms a perception of absolute difference, rendering the stimuli clearly distinct in perceived magnitude (Feigenson et al., 2004). As the ratio diminishes, it becomes increasingly challenging to distinguish between two quantities, so the absolute difference can assist in quantity discrimination. In support of this, we found a notable divergence at different ratio intervals (i.e. ratio ≤ 3 versus ratio > 3). Within the smaller ratio range (ratio ≤ 3), quantity discrimination performance improved as the ratio or

absolute difference increased. In contrast, within the larger ratio range (ratio > 3), the effect of these factors diminished, indicating a differential influence of ratio and absolute difference across the two ranges (Fig. 3). This finding suggests that, across individuals, lovebirds have an average discrimination threshold around a ratio limit (ratio three). However, this threshold varied between individuals. Those individuals who scored a more rewarding overall performance were either better able to differentiate quantities of lower ratios or showed a higher motivation to choose optimally. Such interindividual variation in cognitive capacity can be critical for survival and reproductive success (Cauchard et al., 2013; Cole et al., 2012; Keagy et al., 2009; Rochais et al., 2023). In the wild, rosy-faced lovebirds mainly forage for patchily distributed plants like *Antheophora schinzii* and *Acacia karroo* in arid and semidesert habitats in Namibia (Ndithia & Perrin, 2006a, 2006b). Their capacity for associative learning and quantitative discrimination can help them link landmarks with productive feeding sites, thereby improving their foraging efficiency. In an environment where slight improvements in energy intake could mean survival in times of scarcity, such cognitive adaptation is crucial. Additionally, when competition for resources intensifies, for example during winter, associating with a social group becomes advantageous for foraging and defending territory (Ndithia & Perrin, 2006b). Rosy-faced lovebirds are highly social, and their quantitative discrimination ability likely plays a key role in social activities such as flock foraging and colonial nesting.

CONCLUSION

The general view across cognitive neuroscience, child psychology and animal cognition is that there is a biological capacity specifically evolved for understanding numerical quantities and arithmetic, where quantical cognition (quantity discrimination) provides biologically evolved preconditions for numerical (exact, symbolic) cognition (Núñez, 2017). As with other bird species, most notably Corvidae and Psittacidae, we found that rosy-faced lovebirds were capable of advanced associative learning and quantity assessment. Their quantity discrimination performance was influenced by both ratio and absolute difference, but the effect of these factors depended on the ratio ranges (≤ 3 versus > 3). These findings highlighted the advanced numerical cognition of rosy-faced lovebirds, comparable with that of larger parrot species, and contribute to our understanding of the evolutionary and ecological significance of quantity discrimination in birds.

Author Contribution

Shengyu Wang: Writing – review & editing, Writing – original draft, Visualization, Methodology, Investigation, Formal analysis. **Kevin Ching Hei Lo:** Writing – review & editing, Investigation. **Verna Wing Ting Shiu:** Writing – review & editing, Investigation. **Christy Yuen Ching Hung:** Writing – review & editing, Investigation. **Emily Shui Kei Poon:** Writing – review & editing, Resources. **Chris Newman:** Writing – review & editing. **Christina D. Buesching:** Writing – review & editing. **Simon Yung Wa Sin:** Writing – review & editing, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Conceptualization.

Data Availability

Data and code are available as supplementary material.

Declaration of Interest

The authors have no competing interests.

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Supplementary Material

Supplementary material associated with this article is available at <https://doi.org/10.1016/j.anbehav.2025.123357>.

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