

Article

Salience Beats Individual Cue Preferences

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Simple Summary: Remembering food resources is important for survival. Animals differ in their strategies to remember resources; some use spatial information, and others resource-specific information (colour, shape). Which strategy they use depends in part on their way of life (food-caching species and migratory species prefer spatial information), but is also affected by the salience of the information. Here, we investigated the strategy used in the colour-polymorphic Gouldian Finch by offering spatial and object (feature) cues. Birds were trained to find food either in a white or coloured feeder always positioned in the same location. In experimental trials, feeders were swapped, dissociating the feature and the spatial cues from the feature cue rewarded. Similar numbers of birds preferred the feature or the spatial cue in the first experimental trial, which was not affected by head colour morph, sex or age. However, birds with a spatial preference changed their choices over time, resulting in most birds choosing the feature cue at the end of the experiment. These results indicate that Gouldian Finches have individual preferences for one strategy or the other but can change their preference flexibly depending on the salience of the cue.

Abstract: Animals can use different cues to memorise food resources, which can be broadly divided into spatial and feature cues. Differences in species-specific preferences for spatial or feature cues has been historically linked to their reliance on spatial information (food-caching and migratory species prefer spatial cues), but more recently, attention has shifted to procedural differences largely affecting the salience of cues. Here, we investigated cue preferences in the colour-polymorphic Gouldian Finch to test a range of hypotheses. Birds were trained to find food either in a white or coloured feeder always positioned in the same location. In experimental trials, feeders were swapped, dissociating the feature and the spatial cue from the feature cue rewarded. Similar numbers of birds preferred the feature or the spatial cue in the first experimental trial. Preferences were not affected by head colour morph, sex or age group. However, birds with a spatial preference changed their choices over time, resulting in a significant number of birds choosing the feature cue at the end of the experiment. These results indicate that Gouldian Finches have individual preferences for one cue type or the other but can change their preference flexibly depending on the salience of the cue.

Keywords: associative learning; hierarchical organisation; spatial cues; feature cues; colour polymorphism; sex; age



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1. Introduction

Food resources vary in time and space as well as in appearance. Being able to memorise current food locations can increase foraging efficiency [1,2]. Animals can use a range of environmental cues [3–8], which can be categorised into two main types: spatial cues and featural cues. Spatial cues provide information about the relative or absolute spatial relationships of local and global landmarks and the goal location [9,10], and are often seen as more salient (reliable) cues under stable environmental conditions [10]. Featural cues, in contrast, reflect the appearance of the resource or a close-by beacon such as its colour, shape or smell [11]. Featural cues can help in forming search images and therefore increase

foraging efficiency [10]. Particularly in birds, there are conflicting findings regarding which strategies for memorising resources are used [12].

Numerous studies have shown that animals learn several cues simultaneously, but that they often prefer one cue type over another (hierarchical organization [2,8,12–14]). Other studies have found that the use of cues is flexible and affected by the salience of the cue [3,12]. Historically, cue preferences have been investigated in relation to the ecological demands of a species. For example, species that are especially reliant on spatial information, such as food storing, and migratory birds often prefer spatial over feature cues [4,15,16], whereas closely related species less reliant on spatial information (non-storer) use both types of cues equally [15,16]. However, more recent studies do not confirm this pattern, as food-storing Clark's Nutcrackers (*Nucifraga columbiana*) and Mountain Chickadees (*Parus gambeli*) preferred feature cues [11,17] and Homing Pigeons (*Columba livia domestica*) used feature and geometric (spatial) cues equally [18].

In recent years, attention has shifted to the procedural differences in experiments, explaining some of the discrepancies in results. One example of this is whether cues presented repeatedly or only once affect the salience of the cue. For example, laboratory rats usually prefer feature cues when presented repeatedly. However, when new objects were used for each trial (1-trial associative learning), featural cues became unreliable and the rats used the more reliable spatial cues [2]. Similarly, Rufous Hummingbirds (*Selasphorus rufus*) generally preferred spatial cues even after a single presentation, but switched to feature cues after several repetitions when the locations but not the colour of the flowers changed [19]. Likewise, European Greenfinches (*Carduelis chloris*) preferred feature over spatial cues in one-trial associative learning tasks but spatial cues in repeated trials. Again, the latter was linked to temporally stable environments [10].

The complexity of cues is another factor that can affect cue preferences. Food-storing Mountain Chickadees favoured spatial over feature cues in the Clayton and Krebs [16] study but preferred feature over spatial cues in LaDage et al. [11]. It was suggested that differences in cue complexity caused these opposite results [11], as feature cues were composed of several patterns and colours in Clayton and Krebs [16], while only two colours without patterns were used in LaDage et al. [11]. These studies indicate that besides the effects of ecological demands, other factors such as the salience and complexity of cues affect cue preferences.

Cue preferences differ not only between species but also within species. Intraspecific differences in cue preference have been proposed for sexes again in relation to ecological demands regarding differences in range use (males often range further), brood parasitism (females have to remember host nests) and mate selection based on complex colour patterns. While wide-ranging male rats indeed prefer spatial cues, with no preference in females [20], results in birds are often inconclusive. Male Hummingbirds often outperform females in spatial tasks, but the sexes did not differ in their cue preference [12]. Brood-parasitic female Brown-headed Cowbirds (*Molothrus ater*) have a better spatial memory, but again, no sex differences were detected in learning spatial cues; however, females outperformed males with feature cues [21]. Finally, female guppies (*Poecilia reticulata*) select mates based on complex colour patterns, but no sex differences were found in discrimination learning when feature cues were involved [22].

Beyond differences in sex, few other traits have been investigated. Age differences in cue preference have been found in humans, with young adults preferring featural and older people geometric (spatial) cues [6]. Moreover, there is little known about differences in cue preferences linked to personality, despite cognitive traits having been found to differ between individuals (e.g., [23–25]). Nawroth et al. [26] found that more sociable goats (*Capra hircus*) showed a stronger preference for featural cues and, consequently, better associative learning than less sociable goats. Likewise, no research on cue preferences has been conducted on polymorphic species. Morphs often differ in their diet and micro-habitat use (e.g., [27–29]), which might affect the hierarchical organisation of cue preferences.

In the current study, we investigated cue preferences in the colour-polymorphic Gouldian Finch (*Chloebia gouldiae*). Gouldian Finches' native habitat is in the tropical savannah grassland of North Australia [30]. They are nomadic during the non-breeding season following the availability of grass seeds, particularly Sorghum species, which they pick from the ground or extract from the ear [30,31]. The species is represented by different colour morphs in the same population: red-headed (30%), black-headed (70%) and yellow-headed birds (<1%; [32]). The colour morphs are present in both sexes and signal their personalities [33]. Red-headed Gouldian Finches are more aggressive but less explorative, while black-headed birds are less aggressive but more explorative [33]. Moreover, a recent study about the cognitive differences between Gouldian Finches suggested that black-headed birds invest more in local exploration and information gathering, resembling a resident cognitive style, while red-headed birds are better equipped for the exploration of larger areas, resembling a migratory/nomadic cognitive style [34,35]. However, little is known about the influence of the morphs on foraging strategies in Gouldian Finches. However, Pryke et al. [36] suggested that morphs might differ in their digestive assimilation efficiency, as red-headed birds lost condition under poor nutrition. Red-headed birds might therefore require a higher-quality diet. The combination of different characteristics in this species (nomadic, seedeater, differences among morphs) makes it interesting to investigate whether one characteristic or the other determines cue preferences.

The aim of this study was to determine whether Gouldian Finches rely more on feature or spatial cues in an associative learning task, whether there are differences in the use of these cues between morphs, sexes and age classes, and whether cue selection changes over time. The following predictions were made.

- (1) Species-level predictions:
 - a. As Gouldian Finches feed on scattered grass seeds on the ground or still in the ear, focusing on featural cues would allow them to form a search image [10].
 - b. As a nomadic species, however, they might rely more on spatial cues [4].
 - c. Featural and spatial cues might be used equally based on individual preferences (see also below).
- (2) Intraspecific-level predictions:
 - a. Morphs differ in their cognitive style, with red-headed birds resembling migrants/nomads and black-headed birds resembling residents. Therefore, the former might prefer spatial cues, whereas the latter might prefer feature cues or show no preference [4,18].
 - b. No sex differences were expected linked to differences in range use [20] in this flock-living species.
 - c. We had no a priori predictions for age as so little is known about cue preferences in relation to age.
- (3) Cue preferences over time:
 - a. Preferences might change over time with the salience of the cue [2,10,19].

2. Materials and Methods

2.1. Study Species and Holding Conditions

Twenty-four Gouldian Finches were tested over a period of six weeks. We had 12 females (4 red-headed, 8 black-headed) and 12 males (8 red-headed, 4 black-headed). Ages ranged from 1 to 7 years. All birds originated from eleven different breeders and were purchased over several years. The Gouldian Finches were kept in seven flight cages of 120 cm × 80 cm × 100 cm (length × depth × height) with wire mesh on the front, side and ceiling. Each cage contained a maximum of 6 birds of mixed sex, age and head colour. Six of the seven cages formed double cages, which were connected by an opening (40 cm × 40 cm) allowing the birds to move freely between two adjacent cages. Each cage contained perches, natural twigs, two feed hoppers and a water dispenser attached to the front wire mesh, and a bath on the floor. Food consisted of a mixture of Blattner Amadine

Zucht Spezial (Gouldamadine), Blattner Astrilden Spezial and Blattner rote Mannahirse (Blattner Heimtierfutter, Ermengerst, Germany). Blattner bird grit and eggshells were provided separately. The light regime was 13h of light and 11h of dark.

2.2. Experimental Setup

Whilst still in their flight cages, birds were introduced to the tube-shaped feeders used for this experiment. Birds were food-deprived for one hour before having exclusive access to the new feeders for two hours, after which the original feeders were put back in the cages. This habituation phase lasted seven days with one session per day. Observations assured that all birds were feeding from the feeders at the end of this phase.

Birds were then moved to an experimental room containing six cages of 120 cm × 70 cm × 100 cm (length × depth × height). Only four of them were used in this experiment due to logistic reasons. The front and ceiling of the cages were made of wire mesh, while the walls and floor were made of wood. The arrangement of the cages prevented birds from seeing each other, but they were able to hear each other. Inside each cage were four perches, with two positioned on each of the right- and left-hand sides of the cage. The perches on the same sides were 15 cm apart, and the distance between the perches on the left- and right-hand sides was 55 cm.

Four tube-shaped feeders were attached to the front wire where the perches were located. Each cage had two sets of feeders consisting of one feeder with a white foot and the other with a coloured foot (brown or blue). Colours were balanced across cages and bird combinations (see below). Two sets of two feeders were placed in each cage, with a set of white–brown or white–blue feeders on each side (Figure 1). The two sets in a cage were always of the same colour combination (white–brown or white–blue) and always arranged in the same configuration (e.g., white feeder on the left on both sides of the cage). Across feeders, half the cages had the white feeder on the left side in a set and the other half on the right side in a set.

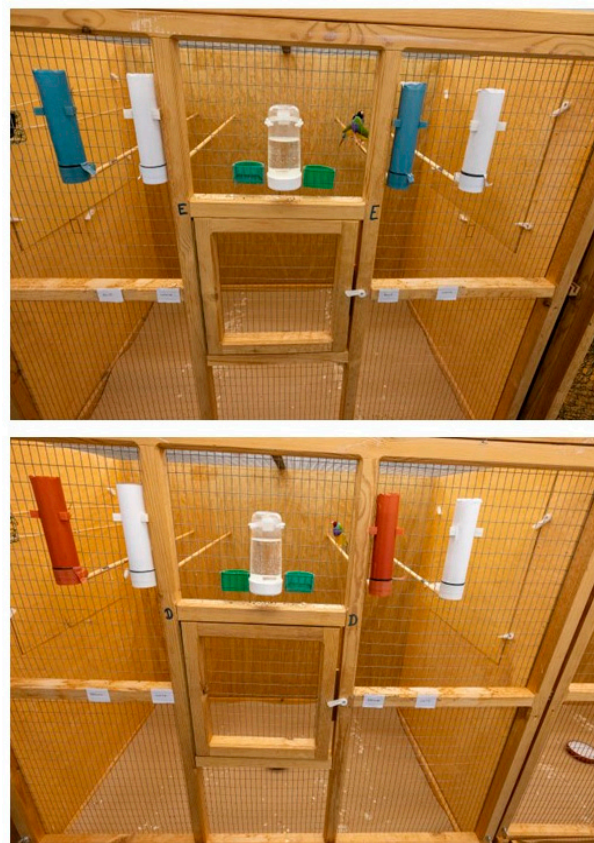


Figure 1. Feeder arrangement.

Each cage had two identical sets of feeders consisting of a white and a coloured feeder. The upper panel shows the blue–white combination, and the lower panel the brown–white combination.

Two sets of feeders were used in each cage as two birds were tested together (see below), with unrestricted access to the feeders of both colours. All perches were marked with a BIC marking pocket pen, 7 cm away from the feeders, delimiting the area where birds were recorded as approaching the feeder. Finally, each cage contained a wire mesh box on the left-hand side to place a camera in for recording the sessions. The cameras used included three GoPro8 Blacks with a wide angle and full high definition and one Crosstour 1080P with full high definition.

2.3. Experimental Procedure

As Gouldian Finches are highly social [32], birds were tested in pairs. Pairs were composed of two birds of the same head colour and sex (four black-headed female pairs, two red-headed female pairs, two black-headed male pairs and four red-headed male pairs). Birds in a pair were at least one year apart, except one pair of same-aged birds, as earlier studies on novelty reactions have shown age effects [37]. Four pairs were tested at the same time, resulting in three rounds of eight birds each. The experiments entailed three parts.

2.3.1. Habituation

On day 1, feeders had their coloured foot, as described above, with the transparent tube allowing the birds to see the food in the feeder (mirroring the feeders used in the holding cages). Cameras were put in the recording cages, after which the birds were released. The recording lasted one hour to check whether birds were eating and drinking. If birds were not eating or drinking, another recording session was carried out, after which direct observations followed of those birds that had not eaten by then. In four cases, another experienced bird was added to encourage eating. All birds ate at the end of day one. All additional birds were removed the next morning.

On day 2, the transparent part of the feeders was covered with coloured paper matching the foot colour to prevent the birds from seeing the food inside the feeders (but food was still easily visible in the feeder foot). The software ‘Paint’ was used to create the coloured papers. Birds were food-deprived for one hour starting at 7:00 a.m.; then, the cameras were placed in the recording cages and the feeders placed in the cages with the coloured papers around the transparent tube. The recording lasted one hour. If birds were not eating, the coloured paper was removed for two hours, making the food in the tube visible again, which resulted in the birds feeding. They were then again food-deprived for one hour, starting at 11:00 a.m., followed by another session with the tube of the feeder covered with paper (1 h recording). All birds ate from the feeder with the coloured paper around the tube at the end of day 2. After this, birds went into the training phase.

2.3.2. Training

On day 3, the feeder foot was covered with a piece of paper with a picture of the seed mixture to prevent the birds from seeing the food. Training to remove the cover consisted of two steps. On the first day of training (day 3), papers partly covered the feeder foot so that birds could still see the food. Once they all removed the covers and ate, the papers were placed to fully cover the feeder opening in the following sessions (day 4 onwards). Two training sessions per day (morning and afternoon) were conducted. The first session started at 7:00 a.m. with one hour of food deprivation, followed by four 30 min trials (8:00–10:00 a.m.) in which the openings of the feeders were covered (partly covered) with the seed picture. Between each trial, the papers were reinstalled on the feeder foot when birds had removed them. At the end of the fourth trials, birds had free access to food for two hours (10:00 a.m.–12:00 p.m.). The second session started at 12:00 p.m. and followed the same steps as the morning session, and ended at 2:00 p.m. At the end of the second session, birds were left over night with free access to food (no cover on the feeder foot). Not all birds

fed with the paper fully covering the feeder foot at the end of day 4. To increase the number of participating birds, changes were made to the pairings. Changes occurred when neither of the two birds in one cage was removing any papers or when one of the two birds was very fast in uncovering the feeders, potentially preventing the other one from removing the paper. Overall, eight birds were swapped once between cages, two in rounds one and two and four in round three. All switches were made between birds of the same head colour. However, in four cases, a male and a female were swapped (one black-headed and one red-headed pair each). The final two swaps were between two birds of the same sex and head colour (one black-headed female pair, one red-headed male pair). Those changes resulted in the following pairings for the rest of the experiment: three black-headed female pairs, one black-headed male pair and two black-headed mixed-sex pairs, as well as one red-headed female pair, three red-headed male pairs and two red-headed mixed-sex pairs. After this change, three pairs were of the same age.

Training with the feeder foot fully covered and the food, therefore, not visible continued until all engaging birds (some birds never removed the paper and were not further considered but left in the cage; see below) consistently removed the cover (removing the cover at least 3 times in the last 4 sessions with the seed paper on the feeder foot). This took until day 9 (group 1), day 6 (group 2) and day 8 (group 3). The birds then moved to the final training stage, where food was removed from one type of feeder (either the coloured or white feeder in each cage). This was balanced across cages, head colours and sex. Birds were left for two days with only one type of feeder providing a reward (but the other one still present in its location) to learn the location/colour of the rewarded feeder. On these two days, training to remove the cover from the feeder foot continued as before. As food was not visible during these training trials, birds had to use their memory to locate the baited feeder. When most birds reached the second criterion (removal of the cover in 3 out of 4 visits to the baited feeder in 1 h), they were considered ready for the tests as they had learned where the food was.

2.3.3. Testing

Birds were tested five times per day for four consecutive days. Birds were food-deprived for one hour (7:00–8:00 a.m.), followed by the first 10 min test where both feeders were returned, with the rewarded feeder only containing a few seeds to prevent fast satiation. All feeder feet were completely covered and the food not visible. After the first test, birds were food-deprived for half an hour before the second test. Tests three to five were all separated by 30 min of food deprivation. For each test, the rewarded feeder was topped up with a few seeds. Two out of five tests were controls with the coloured feeders in exactly the same position as during training. Two tests were experimental conditions with the two feeders next to each other swapped (e.g., the white feeder swapped position with the blue feeder next to it). This brought the colour cue and the spatial cue in conflict. Additionally, the salience of cues changed in the experimental trials to the feature cue as this was the rewarded feeder. The last test was a probe trial in which all seeds were removed from the feeders to test whether birds were using their memory or olfactory cues. Probe trials could be under either control or experimental conditions. Each bird went through 20 tests, 10 control conditions (including two probe trials) and 10 experimental conditions (including two probe trials). For each testing day, the order of the control and experimental conditions was changed. Video recording captured which feeder the birds visited first and removed the cover from.

2.4. Statistical Analysis

Out of the 24 birds, 13 birds consistently removed the cover in five or more control and experimental trials each. Another three birds consistently looked closely at the feeders in five or more control and experimental trials each, but did not remove the cover. Another two birds looked at or removed the cover in three to four control and experimental trials each (seven responses in total), whereas one bird did so only two to three times (five

responses). Five birds never removed any covers and were excluded from the analysis. For the analysis, we used the 13 birds that consistently removed the cover. However, we reran all analyses for 18 birds (those that had at least looked at or removed the cover in three to four control and experimental trials each) to see whether the results could be confirmed with a larger sample size.

For all analyses, the first removal of a paper by each bird in each trial was used. Analyses were conducted with SPSS v26, and data files are available in Table S1. In the first step, to address the species-level predictions (prediction 1), cue preferences were tested by comparing the choices of the birds' first experimental trial in which it responded only, as this reflects the bird's cue preference without any learning that might affect later choices. A Chi-square test was used for testing against chance level ($n = 13$). The test was repeated with a sample size of 19, including all birds that had looked at or removed the cover in at least three experimental trials.

In the second step, we tested whether cue selection changed over time (prediction 3). Proportions of correct first choices in each control and experimental trial were calculated across all birds ($n = 13$). Kendall's tau-b correlations were used to test whether the proportions of correct first choices changed with increasing trial number in the control and experimental situations. Chi-square tests were performed to test whether birds performed better than chance in the control and experimental trials. Every fourth trial (1-4-7-10) was tested to reduce the number of tests. The correct choice in the control trials was choosing the rewarded feeder in the training position and with the rewarded colour (no conflict of cues), whereas in the experimental trials, the correct feeder was indicated by the rewarded colour in the formerly non-rewarded position (bringing the spatial cue and the colour cue into conflict). To test for any effects of olfactory cues, probe trials were analysed ($n = 13$ birds, two trials each for control and experimental trials). Chi-square tests were used to test the birds' performance against chance levels. The above analyses were repeated with the larger sample size of 18 birds, including all birds that had at least looked at or removed the cover in three to four control and experimental trials each (seven or more responses in total).

In the third analysis, we tested whether head colour, sex or age had an effect on cue preferences (predictions 2). Binary logistic regression was used, with the choice of each bird's first experimental trial as the dependent variable and head colour, sex and age as independent variables. Ages were grouped into two categories, one to two years of age and older than two years, to obtain sufficient sample sizes. Analyses were rerun with the larger sample size ($n = 18$).

Ethical Note

Experiments were conducted in accordance with the Association for the Study of Animal Behaviour's ethical guidelines [38] and were non-invasive in nature. Experiments were approved by the University Ethics Committee (CMH_OL/2023-1).

3. Results

Gouldian Finches did not show a significant preference for either of the cues in their first experimental trial (Chi-square test: $\chi^2 = 0.692$, $p = 0.405$, $n = 13$). Five birds went for the feature cue and eight for the spatial cue (Figure 2a). The analysis with the larger sample size provided similar results ($\chi^2 = 0.053$, $p = 0.812$, $n = 19$), with ten birds preferring the feature cue and nine the spatial cue.

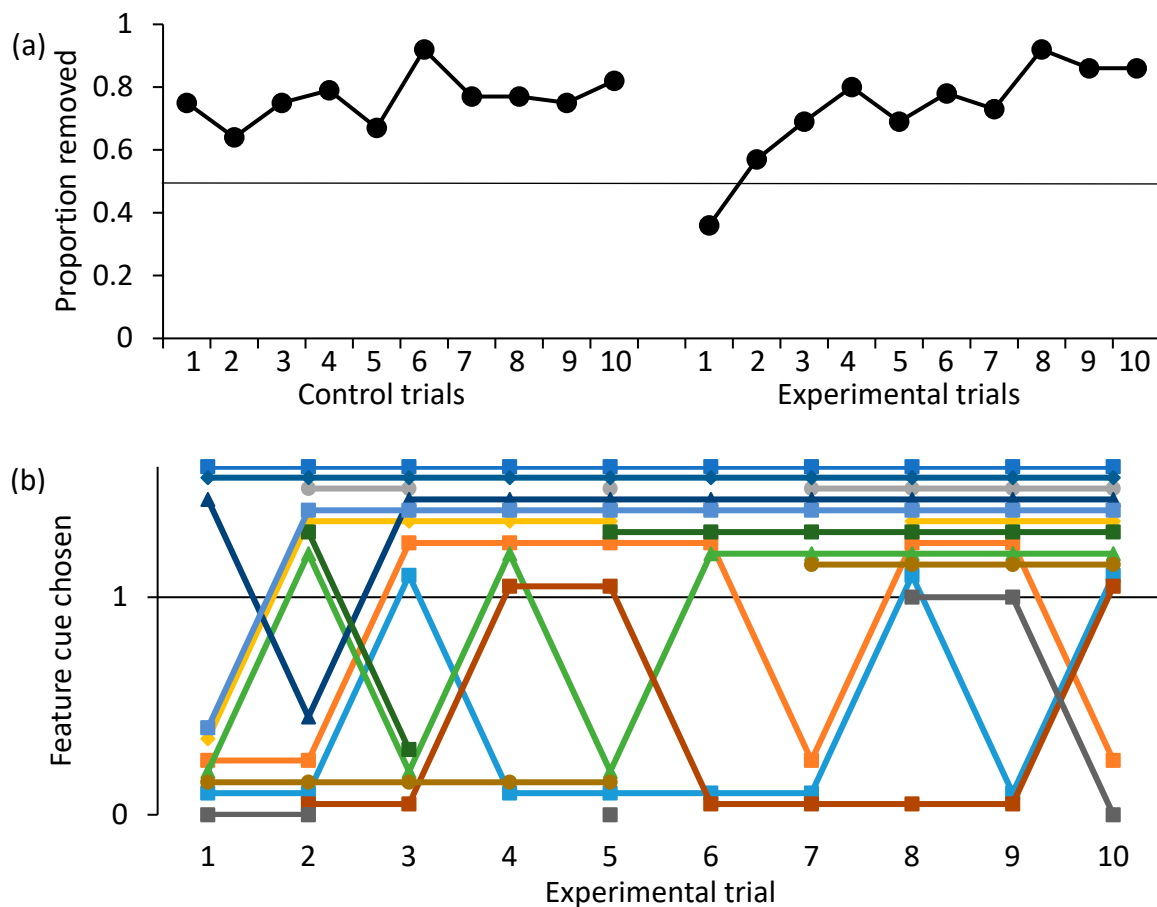


Figure 2. Panel (a) shows the proportion of birds that removed the cover from the correct (baited) feeder first in the control and the experimental (spatial and feature cue dissociated) trials each. Panel (b) shows each individual's first choice made in each experimental trial. Values above 1 represent choosing the correct feature cue, and values below 1 represent choosing the incorrect spatial cue. The data points for correct and incorrect choices are spread out for better visibility. Gaps in a line indicate no choice made in that trial. The colours represent individual birds.

Across all trials, Gouldian Finches consistently chose the correct feeder in the control trial, with a slight but significant increase in correct choices across trials (Kendall's tau-b correlation: corr. coef. = 0.506, $p = 0.046$, $n = 10$ trials, Figure 2a). The proportions of correct choices ranged from 0.64 to 0.92 (mean 0.76). The Chi-square tests of trials 1, 4 and 7 approached significance (trial 1: $\chi^2 = 3.000$, $p = 0.083$, $n = 12$; trial 4: $\chi^2 = 3.769$, $p = 0.052$, $n = 13$; trial 7: $\chi^2 = 3.000$, $p = 0.083$, $n = 12$), with trial 10 being significant (trial 10: $\chi^2 = 4.455$, $p = 0.035$, $n = 11$). In the experimental trials, choices changed significantly from trials 1 to 10 (corr. coef. = 0.719, $p = 0.004$, $n = 10$ trials), with increasing numbers of birds choosing the feature cue as the experiment progressed (Figure 2a). The birds that had gone for the feature cue first consistently did so throughout the experiment, whereas the birds that had chosen the spatial cue first took varying numbers of trials to consistently choose the rewarded feature cue (Figure 2b). The Chi-square tests showed that the birds in trials 1, 4 and 7 exhibited chance performance (trial 1: $\chi^2 = 0.818$, $p = 0.366$, $n = 11$; trial 4: $\chi^2 = 3.600$, $p = 0.058$, $n = 10$; trial 7: $\chi^2 = 2.273$, $p = 0.132$, $n = 11$), with those in trial 10 showing a significant preference for the feature cue (trial 10: $\chi^2 = 6.231$, $p = 0.013$, $n = 13$). When testing performance in the probe trials only, one control probe trial was not significant (trial 5: $\chi^2 = 1.333$, $p = 0.248$, $n = 12$), whereas the other reached significance (trial 8: $\chi^2 = 3.769$, $p = 0.052$, $n = 13$). Likewise, one of the experimental probe trials did not reach significance (trial 3: $\chi^2 = 1.333$, $p = 0.248$, $n = 12$), whereas the other one was significant (trial 10: $\chi^2 = 6.231$, $p = 0.013$, $n = 13$). The analyses with the larger sample size

($n = 18$) resulted in a similar outcome, with the control trials now showing no significant changes in performance over time (Kendall's tau-b correlation: corr. coef. = 0.230, $p = 0.364$, $n = 10$ trials) but with all four tested trials above change level (trial 1: $\chi^2 = 5.400$, $p = 0.020$, $n = 15$; trial 4: $\chi^2 = 6.250$, $p = 0.012$, $n = 16$; trial 7: $\chi^2 = 5.400$, $p = 0.020$, $n = 15$; trial 10: $\chi^2 = 6.231$, $p = 0.013$, $n = 13$). The experimental trials mirrored the results of the smaller sample size, with a significant change over time to increasingly preferring the feature cue (corr. coef. = 0.854, $p < 0.001$, $n = 18$; trial 1: $\chi^2 = 0.067$, $p = 0.796$, $n = 15$; trial 4: $\chi^2 = 2.571$, $p = 0.109$, $n = 14$; trial 7: $\chi^2 = 4.571$, $p = 0.033$, $n = 14$; trial 10: $\chi^2 = 7.143$, $p = 0.008$, $n = 14$).

Cue preference in the first experimental trial was not affected by head colour morph, sex or age class (Table 1).

Table 1. Binary logistic regression to test the effects of head colour morph, sex and age group on cue preference in the first experimental trial for birds that removed the cover ($n = 13$) and for birds that removed or looked at the cover ($n = 18$).

Variable	Birds that Removed the Cover			Birds that Removed or Looked at the Cover		
	df	Wald	<i>p</i> -value	df	Wald	<i>p</i> -value
Constant		0.357	0.550	1	0.649	0.421
Head colour morph		0.007	0.932	1	0.698	0.403
Sex		0.027	0.870	1	0.000	0.986
Age class		0.416	0.519	1	0.789	0.374

df: degrees of freedom.

4. Discussion

Gouldian Finches did not prefer a particular cue, but individual preferences were split into equal use of the spatial and feature cues in the first experimental trial. However, as the experiments progressed, the salience of the cue in the experimental trials changed choice behaviour in birds that had a preference for the spatial cue. Neither head colour nor sex nor age influenced cue preferences.

Not all birds engaged in the task, which was in part down to their partner being too fast in removing the covers. This was addressed in part by re-pairing the birds, which resulted in some of them taking part in the experiments. However, others never engaged, which is not unusual for learning experiments (e.g., [10]). The main analysis was conducted with birds that consistently removed the cover ($n = 13$), choosing a conservative approach. However, the results were confirmed when including birds that had looked at the cover, increasing the sample size to $n = 18$. Additionally, partners might have influenced each other in their choices. This was not the case, as in half the cages, the two birds chose the same, and in the other cages, the partners chose opposite cues. Moreover, the learning curve in those birds that preferred the spatial location indicates that partners in a cage did not influence each other, as one would have expected a faster switch. We therefore believe that the results are representative.

Our first prediction (1a) was that Gouldian Finches might prefer feature cues due to feeding on scattered seeds, which would allow them to form a search image [10]. Five birds went for the feature cue in their first experimental trial and also thereafter, whereas eight birds went for the spatial cue first. Therefore, Gouldian Finches do not seem to use feature cues as their preferred strategy. The equal use of cues on the species level confirms prediction 1c and is in agreement with other studies on non-caching seed-eating birds such as Dark-Eyed Juncos (*Junco hyemalis*; [15]), Blue Tits (*Cyanistes caeruleus*), Eurasian Jackdaws (*Corvus monedula*; [16]) and Pigeons [18]. However, it is in contrast with findings

in European Greenfinches [10], another non-caching seed eater, which initially preferred feature cues.

Our second prediction (1b) forecasted a preference for spatial cues due to the nomadic behaviour of Gouldian Finches [4]. This prediction was not confirmed. While eight of the thirteen birds went for the spatial location in their first experimental trial, indicating some preference for spatial cues, this was not significant. Moreover, two of those birds switched to feature cues from the second experimental trial onwards, indicating low or no preference for either cue. Nonetheless, the remaining six birds seemed to prefer spatial cues as they repeatedly went for the spatial cue, despite finally going for the feature cue. It cannot be ruled out that this preference is down to lateralisation [39] as in the control situation, food was always provided in the same spatial location for a given bird. Future studies should account for this.

While Gouldian Finches do not show a general preference for feature or spatial cues, individual preferences might be affected by the specific characteristics of a bird. Prediction 2a entailed that head colour morphs, which represent resident or nomadic cognitive styles, respectively, affect cue preferences, with black-headed birds potentially going for feature cues and red-headed birds for spatial cues [34,35]. However, no effects of head colour/cognitive style on cue preference were found. Overall, these results contrast with spatial cue preferences in nomadic Pine Siskins (*Spinus pinus*; [4]). Likewise, sex did not affect cue preferences, confirming prediction 2b, as we did not expect any sex differences in cue preference in this flock-living species. This is consistent with Becu et al. [6] and Hodgson and Healy [40]. Sex differences in strategy use are often linked to differences in ranging behaviour (e.g., [20]), which is unlikely the case in Gouldian Finches. Finally, age classes did not affect cue preferences (prediction 2c). Very few studies have investigated age effects, and the only study we found showed a change in cue use in older people linked to age-related decline in navigational abilities [6].

Gouldian Finches changed their preferences with the progression of the experiment, indicating flexible cue use [12]. While there was no significant cue preference across all individuals at the beginning of the experimental trials, birds showed a learning curve and significantly preferred the feature cue at the end. This shows that the birds paid attention to the salience of the cues. Initially, both the spatial and feature cues were reliable, and birds used their preferred cue. However, with the dissociation of the cues during the experimental trials, the feature cue became more salient, as the food was always delivered in the feeder with the same colour but in a changed position. That birds pay attention to the salience of a cue and adapt their strategy accordingly has been shown in a range of species [2,4,10,19] and seems to be one of the more consistent results found across species. The relatively quick change in preference across trials in some of the Gouldian Finches might indicate that the birds learned both cues with a hierarchical organisation of cue use [1–3,8,12,13]. Interestingly, birds with an initial preference for the spatial cue took varying numbers of trials to switch to the feature cue. Two birds consistently chose the feature cue from their second experimental trial onwards, whereas the others were still inconsistent at the end of the experiment. Whether this reflects different strengths in cue preference or differences in re-learning ability requires further investigation.

5. Conclusions

In conclusion, Gouldian Finches pay attention to a range of cues but use a hierarchical organisation, with some individuals preferring spatial cues and others feature cues. Cue use is flexible, and birds adapt their strategy to the salience of the cues. Birds do not differ in their cue preference due to head colour morph, sex or age.

Supplementary Materials: The following supporting information can be downloaded at: <https://www.mdpi.com/article/10.3390/birds5010008/s1>, Table S1: Data file.

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