The role of personality traits in pair bond formation: pairing is influenced by the trait of exploration

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Abstract

In species with long-term pair bonds, such as zebra finches, evaluating the quality of potential mates is critically important. Courtship is an opportunity to evaluate information from dynamic behavioural cues. Personality traits, as stable individual differences in behaviour, could predict the quality of a potential mate. How might personality traits influence mate choice? We examined the influence of several personality traits, including exploration, aggression, and social preference, on pair formation in zebra finches. We provided birds with a variety of potential mates and allowed them to select a pair partner. Our semi-naturalistic mate choice paradigm allowed birds to observe social information over an extended period, simulating the challenges of social evaluation that birds encounter in the wild. We found that pairing is influenced by personality, with birds selecting mates similar to them in exploration. The partner's exploration score relative to their own was more important than the absolute exploration score.

1. Introduction

What behavioural traits are key when selecting a mate? In some species, high levels of certain traits may prove attractive regardless of other social or contextual factors. For example, female guppies prefer males with more orange spots (Houde, 1987), and might settle for pairing with less attractive individuals only if they are unable to obtain a highly spotted mate. Alternatively, individuals might select a mate relative to their own traits. White-throated

sparrows occur in two plumage morphs and typically mate with an individual of the opposite coloration (Tuttle, 2003).

Traditionally, studies of mate choice focused on morphological traits and sensory biases (Ryan & Keddy-Hector, 1992). For example, in a highly-cited book on mate choice (Bateson, 1983), nine out of twelve chapters devoted to traits important for mate choice focused on physical characteristics such as size, plumage coloration, and auditory or olfactory signals, while only three included discussion of behaviours, such as parental care, playing a role in mate choice equal to physical appearance. More recently, however, the functional significance of behavioural traits in studies of mate choice is receiving increasing attention. Dynamic behavioural cues that are responsive to environmental changes, yet largely stable across contexts, might provide more insight into mate quality than static morphological cues. The present study examines the role of behavioural traits relative to individual mate choice in zebra finches, with the goal of examining whether personality traits predict mate choice and pair bond formation within naturalistic groups.

Zebra finches (*Taeniopygia guttata*) are small Australian songbirds frequently studied in the context of mate choice (reviewed in Riebel, 2009). Despite thorough examination, it remains unclear how zebra finches select their mates. Zebra finches do not appear to choose their mate based on overall body condition or physiological quality (Wang et al., 2017), or by their overall size (Wang et al., 2019). Moreover, there is very little agreement between females as to male attractiveness (e.g., body mass, ornamentation, song rate; Forstmeier & Birkhead, 2004). While females undoubtedly indicate preferences among mates, the factors driving these preferences remain unknown.

What, then, can explain the high degree of variability when zebra finches select a mate? One potential approach is to examine behavioural traits, to see whether intrinsic differences in behavioural tendencies influence mate choice. When taking the traits of both individuals into account, a different picture emerges. Females appear to prefer mates that match them, with exploratory female zebra finches selecting exploratory males (Schuett et al., 2011b; though cf., Schielzeth et al., 2011). In monogamous species that rely on equal contributions from both parents to raise their altricial young, individuals might assess potential mates both on the basis of their quality as a future parent (e.g., Munson et al., 2020), and on their behavioural compatibility as a pair (e.g., Ihle et al., 2015).

Personality traits, commonly defined as consistent individual differences in behaviour over time or across contexts (Réale et al., 2007), may provide a means to index the compatibility of a potential mate. Previous studies have examined the interplay between animal personality and sexual selection (see Schuett et al., 2010, for a review). While selecting a mate relative to their own traits, animals may indicate preferences for mates that are similar to them (positive assortative, or assortative mating), or exhibit a preference for individuals that are dissimilar (negative assortative, or disassortative mating). For example, individuals may pair assortatively (orb weaving spiders, Kralj-Fiser et al., 2013) or disassortatively (cockatiels, Fox & Millam, 2014; giant pandas, Martin-Wintle et al., 2017) by aggression, and assortatively (dumpling squids, Sinn et al., 2006) or disassortatively (rainbow kribs, Scherer et al., 2017) by boldness. Moreover, exploratory male great tits may prefer exploratory females (Groothuis & Carere, 2005) and pairs can achieve greater reproductive success through assortative mating (Both et al., 2005).

Zebra finches display personality traits, including exploration and aggression (Schuett et al., 2011a). Here, we assessed zebra finches on exploration in a novel environment, aggression in a mate-competition context and upon introduction to a potential pair partner, and social preference for novel or familiar same-sex conspecifics. Our selected personality traits may influence mate choice. For example, high exploring females indicated a preference for exploratory males in a two-way choice-chamber test (Schuett et al., 2011b). Pair behavioural compatibility may play a role in zebra finch reproductive success, as birds that were allowed free choice of mates exhibited greater success in raising offspring than birds that were assigned a mate (Ihle et al., 2015). Additionally, when birds were assigned a mate with similar exploration scores and similar consistency in exploration, they raised young in better condition at fledging (Schuett et al., 2011a). Therefore, we predict that birds would exhibit a preference for mates similar in personality traits.

However, most examinations of the relationship between personality and mate choice have either measured personality traits after pair formation, randomly assigned birds to pairs and then examined differences in reproductive outcomes, or assessed preferences indicated prior to pairing, but not the full period of pair formation (though see Schielzeth et al., 2011). Measuring personality traits after pair formation leaves open the possibility of behavioural convergence throughout the duration of the pair bond, as individuals might grow to resemble their mates (Ouyang et al., 2014; Laubu et al., 2016). Thus,

in the current study, we measured personality traits prior to pair formation and observed the full courtship period, to better assess whether birds mated assortatively.

We used a semi-naturalistic method that maintained a complex social environment for the entirety of the courtship period. By providing a variety of individuals, we let the birds acquire information about potential mates in social contexts resembling the flock structure of wild-living birds. Our mate-choice method allowed for more naturalistic pair behaviours to occur, as zebra finches in the wild typically breed in flocks of 7–47 pairs (Zann, 1996), and thus would presumably select between a variety of potential mates. Individuals could observe a constellation of naturally occurring behaviours in potential mates over the course of weeks, and participate in proximal social interactions, both aggressive and affiliative, as they selected a mate from multiple different options. Any resulting mate choice would then be based on a rich dataset of experienced interactions, more similar to how zebra finches would pair with other flock members in the wild.

Our method of allowing birds to freely pair complements the typical paradigm, which uses a multi-choice-chamber test (Rutstein et al., 2007; David & Cézilly, 2011; Schuett et al., 2011b; Holveck et al., 2011). In the multi-choice chamber paradigm, an individual is given the choice between potential mates that ideally differ only in one trait (e.g., beak redness or exploration) and the focal animal's preference is assessed based on their position relative to the opposite-sex stimuli. An animal that selectively spends more time near one potential mate is judged to have formed a preference. Choice-chamber tests have provided invaluable contributions to understanding the role of personality traits in mate choice, especially in experiments where an individual's apparent personality can be manipulated (Schuett et al., 2011b). While this paradigm is undoubtedly useful when considering the influence of a single trait on mate preference, it remains unclear how individuals might weigh the relative importance of a trait during mate selection in a group situation where social dynamics might influence mate choice, such as flocks in the wild.

Using our free-choice paradigm, we tested whether zebra finches exhibit assortative mating by personality traits under naturalistic conditions, as a means to validate existing mate-choice assays. There were three potential outcomes. First, individuals might reach a consensus in terms of what personality traits are attractive in a potential mate (e.g., rainbow krib females

prefer males that are predictable in aggression, Scherer et al. 2018). In this absolute trait scenario, individuals with high scores in a given trait would be favored as mates, with a reduced latency to pair, and individuals with low scores in a given trait would remain unpaired, or take longer to pair than high scoring individuals, as they would be less preferred as mates. Second, individuals might select a mate relative to their own personality traits, potentially to maximize behavioural compatibility (e.g., cockatiels mate disassortatively by aggression, Fox & Millam, 2014), resulting in a correlation between their scores on a given trait. In this relative trait scenario, more correlated individuals would be expected to pair faster, and we would expect no significant differences in personality between paired and unpaired individuals. Finally, certain personality traits may not relate to mate choice. If, for example, our personality tests do not capture traits that are relevant to zebra finches during mate choice, or the selected personality traits are not important to mate choice, we would expect no relationship between mate choice and personality trait.

We predicted that individuals would follow the relative trait scenario described above, exhibiting a preference for mates with similar personality traits. From previous studies establishing the importance of exploration in this species, we also hypothesized that exploration, in particular, would be an important trait in regards to mate selection, and might drive mate choice more than aggression or social affiliation.

2. Materials and methods

2.1. Subjects and housing

We tested 48 unpaired, reproductively naïve adult zebra finches, and observed the resultant pairs ($N = 16$), as some birds did not form a pair bond. Prior to commencing the study, two cohorts were planned in order to allow for time constraints on running a battery of personality tests. The first cohort of 20 birds (10 female) was tested in 2015, and a second cohort, consisting of 20 birds (10 female), was tested in 2016. However, when few pairs formed in the second cohort, we additionally tested four more males and females and added them to the large breeding aviary, as the focus of this study was on pair bond formation. This brought the total numbers of the second cohort to 28 birds (14 female). All birds were from domestic stock,

either obtained from Magnolia Bird Farms or produced from our own breeding colony at Cornell University (originally bred from Magnolia Bird Farms stock), with wild-type plumage. The colony was kept indoors on a 14-hour light:10-hour dark photoperiod cycle at constant temperature (22°C) with 40–50% humidity. Within the colony, birds were supplied with ad libitum food (Kaytee FortiFinch Food), water, cuttlefish bone, and grit, with supplemental vegetables provided twice per week. All procedures were approved by Cornell's IACUC committee under protocol 2014-0025.

During personality testing, birds were housed in same-sex aviaries (1.2 × 0.9 × 0.6 m, height × width × depth) in groups of 12–16 individuals, including both focal birds and same-sex stimulus birds used in the personality tests. All birds of each cohort were kept in the same room. However, males and females were not located in adjacent aviaries within the room, preventing visual contact prior to mate choice.

2.2. Personality tests

All personality tests were conducted between 11:00–13:00 h in order to prevent differences in activity levels or behaviour due to circadian rhythms. In all tests, birds were visually and acoustically isolated from the colony, to avoid any changes in behaviour that might result from interacting with non-stimulus conspecifics. We first tested all birds on exploration (Figure 1). Next, we tested aggression towards same-sex and opposite-sex individuals, and social preference for novel or familiar conspecifics, in a counterbalanced order, with at least 24 hours separating each test for each bird to avoid any carryover effects from the previous test. Last, we tested exploration once more, to assess behavioural stability for this trait within individuals. The second exploration test was conducted two months after the first; an ecologically relevant span of time, as that is roughly the period of pair coordination that must occur from nest construction to raising offspring to independence. In all, personality tests spanned March–May 2015 for Cohort 1, and October–December 2016 for Cohort 2.

2.2.1. Exploration
Exploration was assessed in a novel environment test, similar to Schuett et al. (2011a), in an aviary (1.2 × 0.9 × 0.6 m) visually and acoustically isolated from their typical housing. Birds were tested individually, which can be stressful for highly gregarious species. In order to alleviate
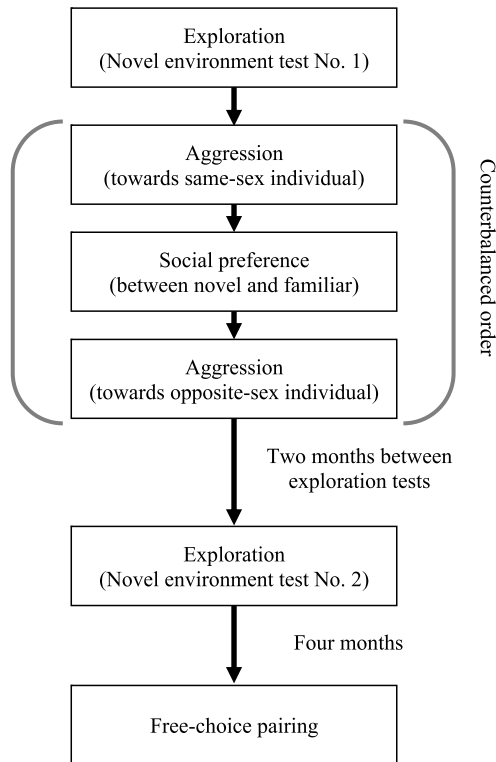
Figure 1. Experiment timeline. Individuals were first tested on a variety of personality traits, including exploration, aggression towards opposite-sex and same-sex conspecifics, and social preference for novel vs. familiar individuals. Each bird was tested twice for exploration, with two months (during which the birds were tested on the other traits) separating the two exploration tests, to assess stability of that trait. Once all the birds in each cohort were tested, they were placed within a single, large aviary and allowed to select a pair partner over a period of three weeks. As pairs formed, they were removed from the pairing aviary, to encourage unpaired birds to select a mate.

any behavioural change due to isolation, we played a background recording of aviary sounds. The speaker was centred underneath the test aviary to prevent the birds from localizing the source and becoming attracted to a specific side of the aviary (Figure A1 in the Appendix). Recordings were played at 65–75 dB, measured from within the centre of the test aviary, comparable to the loudness of zebra finch calls within the communal housing and to stimuli used in previous studies involving zebra finch vocalization playback (Spencer et al., 2005). The background aviary recording was suffi-

cient to allow resumption of typical, non-stressed behaviours (e.g., preening, singing, hopping). The test aviary was the same size as their home aviary, but in a different orientation and filled with a novel configuration of unfamiliar perches. Each perch (referred to as 'feature' for analyses) consisted of multiple branches ('components'). We recorded six different variables that measured exploratory behaviour: latency to commence exploration — that is, the length of time before an individual first landed on a novel feature or component — and the total number of features and components, both novel and repeat, that each bird visited within a 5-min window. Birds could visit up to 5 novel features, and up to 20 novel components. If a bird did not explore, latency to explore was recorded as the maximum, 300 s (5 min). Birds were re-tested for exploration two months after their first test. The configuration of perches was different between each test to keep the environment novel; the order in which birds were tested in each configuration was counterbalanced.

2.2.2. Aggression

Aggression was assessed in two different contexts: a mate-competition paradigm, examining aggression towards a same-sex competitor, and when birds first encountered an opposite-sex potential pair partner, measuring aggression towards an opposite-sex individual. Food, water, and cuttlebone access were provided ad libitum for the duration of these tests.

2.2.2.1. Same-sex aggression. In the mate-competition paradigm, similar to Goodson & Adkins-Regan (1999), birds were first allowed a habituation period to interact with an opposite-sex potential pair partner placed in an adjoining cage (both cages $0.4 \times 0.36 \times 0.43$ m). After the 30-min habituation period, a same-sex competitor was added to the cage of the focal bird. Aggressive interactions during a 5-min period were recorded, including threat postures, beak fencing, pecking, and displacements (Morris, 1954; Zann, 1996). Threat postures typically precede an aggressive interaction such as a peck or displacement, wherein the aggressor crouches horizontally on the perch with sleeked plumage and their body oriented directly towards the opponent. Beak fencing involves two upright birds 'fencing' with closed beaks, usually striking towards the head of an opponent. Pecks were recorded when one bird successfully pecked (made contact) with the body or feathers of another bird. Displacements ('supplanting attacks'; Zann, 1996) involve one individual displacing another from their perch after an aggressive encounter.

2.2.2.2. Opposite-sex aggression. Aggression directed towards potential pair partners was also examined. In this test, the focal bird was placed in a cage (0.4 × 0.36 × 0.43 m) and given 30 min to habituate, with a background recording of aviary sounds playing in order to alleviate any stress due to isolation. At the end of the habituation period, an opposite-sex stimulus was introduced. We scored aggressive interactions towards the opposite-sex stimulus, as above. Since aggression towards an opposite-sex bird was relatively rare, with low frequencies of each of the types of aggressive behaviour described above, these scores were transformed into a binary variable of whether aggression occurred.

2.2.3. Social preference

We also assessed social preference for novel or familiar same-sex conspecifics, as in Kelly & Goodson (2014). In this test, the focal bird was placed in a cage (0.6 × 0.36 × 0.43 m) between two cages (0.4 × 0.36 × 0.43 m) each containing two birds. Familiar birds were drawn from the home aviary of the focal individual, while novel birds were ones that they had never previously interacted with. The preference cage contained a perch marked with different colours at 5-cm intervals, in order to accurately determine the position of the focal animal, with easily identifiable 'social zones' marked within 15 cm of each end. The side containing novel conspecifics was counterbalanced across birds. If individuals did not meet the pre-determined criterion of visiting each social zone at least once during the 5-min period, they were re-tested. If birds still did not meet the criteria during the re-test, it was difficult to assess whether they were indicating a preference of one side over the other, and their data was excluded from further analyses. Preference for novel or familiar conspecifics was determined by dividing the duration of time in one zone by the total duration of time in both social zones (e.g., duration of time with novel conspecifics/duration of time near novel + familiar conspecifics).

2.3. Behavioural coding

All recorded videos were coded for the specified behaviours using ELAN behavioural coding software, created by the Language Archive at the Max Planck Institute for Psycholinguistics in Nijmegen, The Netherlands (version 4.9.4, https://tla.mpi.nl/tools/tla-tools/elan/; Sloetjes & Wittenburg, 2008). ELAN allows for behavioural coding that is time-locked and accurate to each frame of video.

2.4. Mate choice determination

Four months after the personality tests were concluded, all zebra finches in each cohort (equal numbers of each sex) were placed into a large inter-connected aviary (1.2 × 1.8 × 0.6 m) and allowed to freely pair. Video recordings were conducted for one hour every morning. These videos were then coded with ELAN for affiliative pair behaviours of interest: clumping, where birds sit with their feathers touching, and allopreening, where one individual preens another. These behaviours served as our criteria for pair formation, established in previous studies with this species (Butterfield, 1970; Silcox & Evans, 1982): on the fourth non-consecutive instance that the same two individuals were found clumping, they were recorded as having paired. Clumping has been found to predict other pair behaviours, such as vocal exchanges (D'Amelio et al., 2017), and is frequently used in the literature as a behavioural indication of pairing (e.g., ten Cate, 1985; Zann, 1996; Tomaszycki et al., 2006; Pedersen & Tomaszycki, 2012). Pairing latency was defined as the duration between placement in the interconnected aviary and the time at which two individuals were classified as a pair. After pairs were established, they were relocated to a different aviary, to encourage unpaired individuals to direct their attention towards available potential mates.

2.5. Statistical analysis

All analyses were performed in R version 4.0.1 (R Core Team, 2020). Exploration was normally distributed, however all remaining personality traits (aggression and social preference) were non-normally distributed (Shapiro–Wilk W-test, all $p < 0.04$), confirmed via examination of normal quantile plots. Therefore, all analyses involving these variables used nonparametric statistics.

2.5.1. Repeatability of exploration

As in previous studies (David et al., 2012b; Schuett et al., 2011b), we measured exploration twice in order to assess the consistency (i.e., repeatability) of that trait over time. The elapsed time between the two exploration tests (approximately 2 months) was comparable to an ecologically relevant span of time; roughly equivalent to the duration of mate choice, nest construction, and rearing chicks to nutritional independence.

    As mentioned above, each assessment of exploration involved six different variables (latency to explore, number of novel visits, and number of repeat

Table 1.

Descriptive statistics for exploration in male and female zebra finches.

Sex	N	Components			Features		
		Novel	Repeat	Latency to novel (s)	Novel	Repeat	Latency to novel (s)
Females	24	2.1 ± 1.8	4.8 ± 6.4	105.0 ± 91.6	1.9 ± 1.3	3.0 ± 3.9	101.7 ± 106.0
Males	24	3.7 ± 2.2	7.4 ± 5.3	50.0 ± 73.4	2.6 ± 1.3	5.0 ± 4.8	55.0 ± 74.6

Values are means $\pm$ SD, averaged across the two novel environment tests. The exploration score is the number of novel components or features visited, and the activity score is the number of repeat components visited.

visits; each for both features and components: Table 1). In order to simplify the data for analysis of consistency, we first transformed the data to Z-scores, so that the scales were comparable. Internal consistency of the six exploration variables was high at each time point (calculated using the 'psych' package in R; Revelle, 2020) (Time 1: Cronbach's $\alpha = 0.89$; Time 2: Cronbach's $\alpha = 0.89$), above the general cut-off of 0.7 or 0.8 (Bland & Altman, 1997), indicating that it was appropriate to collapse across the variables for the purpose of analysis. We averaged the scores across the six exploration variables to achieve a single index score for each bird at each time point — and in order to use a measure of behavioural repeatability that could be compared with previously published studies. Then, we calculated repeatability using the 'rptR' package in R (after Stoffel et al., 2017) via generalized linear models, with the exploration score as our dependent variable, sex and cohort as fixed effects, and individual as a random effect.

2.5.2. Principal component analysis on exploration

Once we established the repeatability of exploration over time, we next titrated out the contributions of various behavioural measures to the overall exploration score using a principal component analysis. Of our selected personality traits, exploration was the only one with more than three measured variables. In order to create index variables of exploration, and reduce the number of multiple comparisons necessary to determine if assortative mating occurred, we included all of our measured exploration variables in a principal component analysis. The first principal component (PC1) loaded primarily on average novel features and novel components visited, while the second principal component (PC2) included latency to visit novel compo-

Table 2.

Principal components loadings of the exploration variables.

	PC1	PC2
Novel components	*−0.45*	0.19
Repeat components	−0.39	0.31
Latency to novel component	*0.41*	*0.46*
Novel features	−0.44	−0.05
Repeat features	−0.35	*0.61*
Latency to novel feature	0.40	*0.54*
Eigenvalue	4.04	0.71
% variance explained	63.7	11.8

Behaviours with the strongest contribution to each component (> 0.4) are shown in italics. Total variance explained via first two components $= 75.5\%$.

nents and features, as well as repeat features visited (Table 2; Figure A3 in the Appendix).

Next, we plotted the scores of individual birds in the principal component space to assess whether individuals differed by cohort or sex. This served as an additional check on our decision to pool the cohorts in further analyses. They did not cluster by cohort (Figure 2) and there were no statistically significant differences between cohort means on PC1 (one-way ANOVA: $F_{2,45} = 1.104$, $p = 0.3403$) or PC2 (one-way ANOVA: $F_{2,45} = 0.815$, $p = 0.449$). Thus, the two cohorts did not appear to differ in the exploratory types of birds present, confirming our decision to pool the data across cohorts for analyses.

2.5.3. Assortative mating

In order to determine whether birds were selecting their mate based on personality traits, we conducted correlations between the scores of males and females within a pair. Specifically, we examined whether there were significant correlations between pair partners on the two exploration principal components (PC1 and PC2), our aggression variables (duration and latency), and the social preference of individuals. As there were multiple correlations tested, we adjusted the *p*-values to account for multiple comparisons using Benjamini & Hochberg's (1995) 'false discovery rate' method.
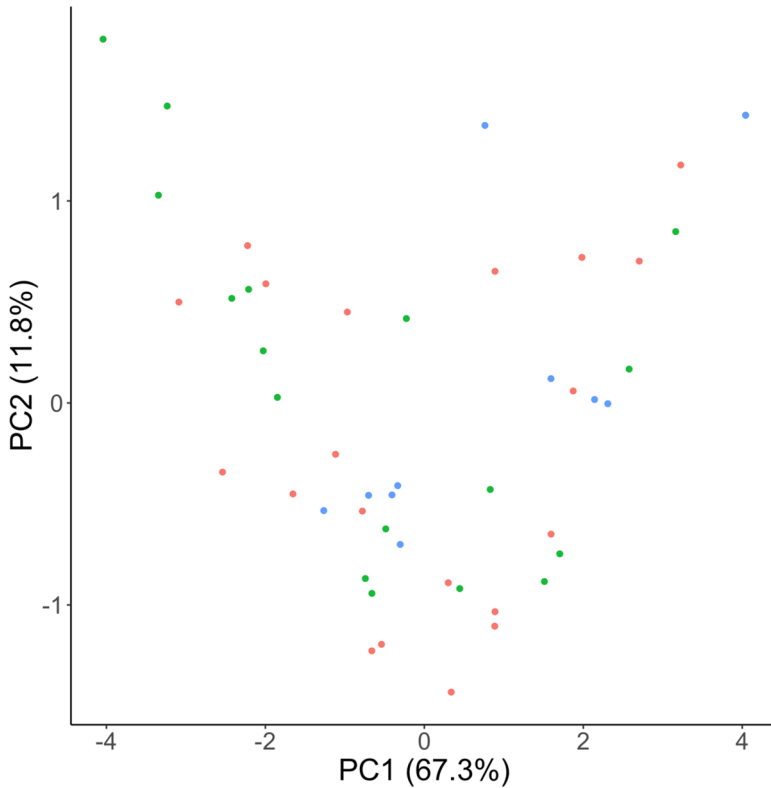
Figure 2. The exploration scores of each individual on PC1 and PC2 across cohorts. Colours indicate cohort (red for Cohort 1, green for Cohort 2, blue for supplemental birds added to Cohort 2). As can be observed, data from each cohort overlap in the principal components space, confirming our decision to pool data across components.

3. Results

Overall, no significant differences between the cohorts on exploration, aggression, or social preference were observed (one-way ANOVAs conducted across cohorts for each variable, all p values > 0.05). The data from both cohorts were therefore pooled together for subsequent analysis.

3.1. Exploration

Exploration scores remained consistent (i.e., were significantly repeatable) across time ($R = 0.489$, 95% CI: [0.264, 0.698], $p = 0.001$). Therefore, scores were averaged across the two time points for subsequent principal component analysis.
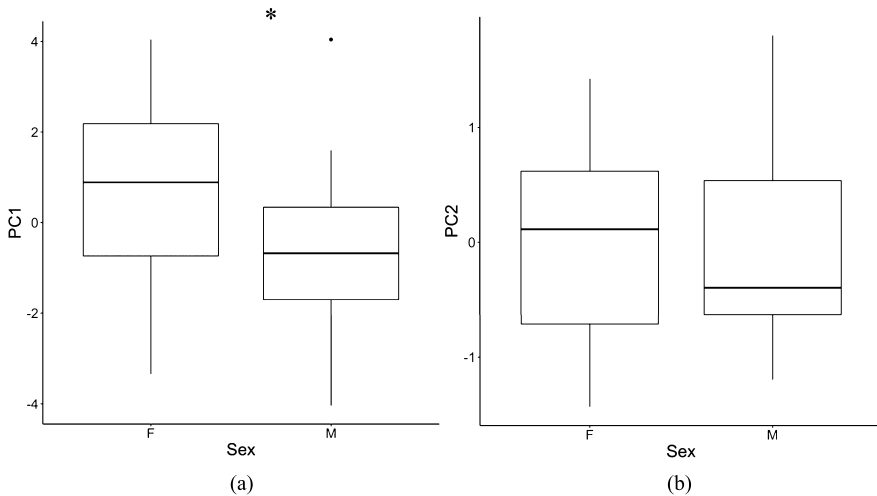
Figure 3. Sex differences in the principal components. (a) Females score significantly higher in PC1 than males, but (b) there is no difference between the sexes in scores on PC2.

Our PCA on the variables measured in the novel environment test revealed sex differences in the retained principal components. Namely, females scored significantly higher than males on PC1 ($t = 2.40$, $N = 48$, $p = 0.021$) — in other words, from the loadings on the principal components, females in general visited fewer novel components and features, and took longer to visit the first novel component. There were no sex differences in PC2 ($t = 0.19$, $N = 48$, $p = 0.85$) (Figure 3). There were also no differences between birds that eventually paired and those that remained unpaired in terms of exploration, either for PC1 or PC2 (all p values > 0.248; Figure 4).

3.2. Aggression

Males and females did not differ in aggression (Table 3). There was no significant difference in latency to aggression between males and females (Wilcoxon rank sum test: $W = 361$, $N_1 = 24$, $N_2 = 24$, $p = 0.123$), nor in duration of aggression (Wilcoxon rank sum test: $W = 224$, $N_1 = 24$, $N_2 = 24$, $p = 0.176$). When examining likelihood of aggression towards an opposite-sex pair partner, there were no significant differences between males and females (Chi-square test: $\chi_1^2 = 2.14$, $p = 0.143$).

There were no significant differences between birds that eventually paired and those that remained unpaired in terms of latency to aggression (Wilcoxon
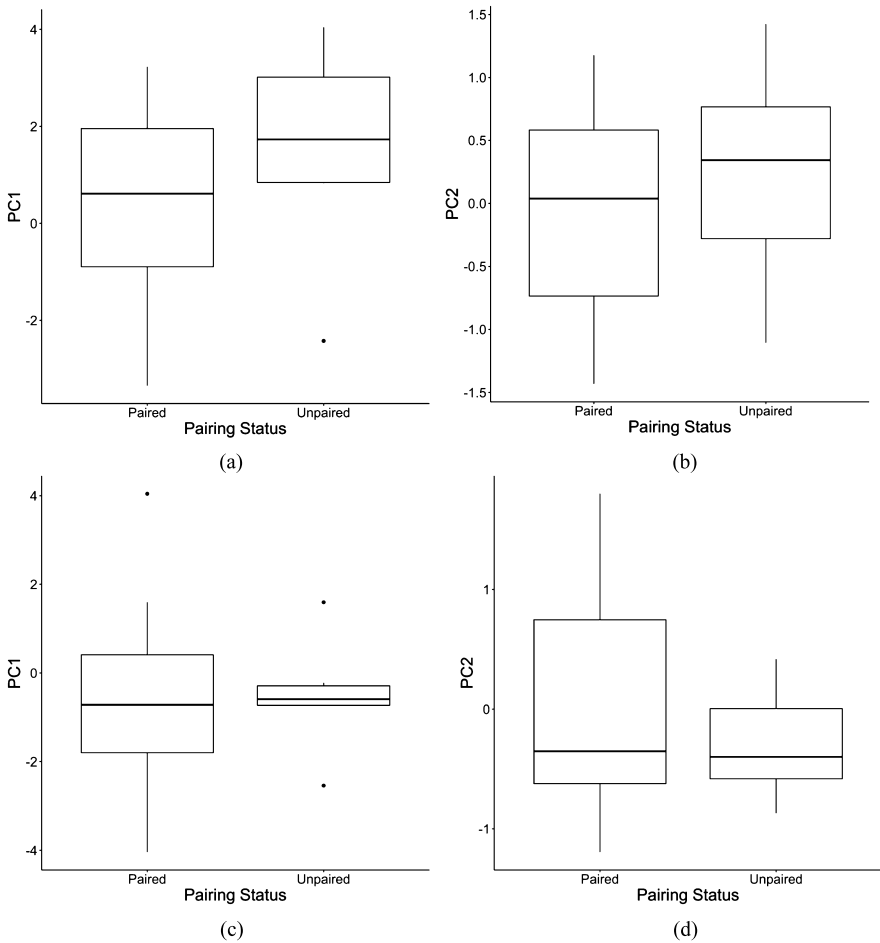
Figure 4. Paired and unpaired birds do not differ in exploration. There was no significant difference between paired and unpaired females for (a) PC1 or (b) PC2, nor was there a significant difference between paired and unpaired males for (c) PC1 or (d) PC2.

rank sum test: $W = 206$, $N_1 = 36$, $N_2 = 12$, $p = 0.815$; Figure A4 in the Appendix) or duration of aggression (Wilcoxon rank sum test: $W = 241$, $N_1 = 36$, $N_2 = 12$, $p = 0.547$; Figure A5 in the Appendix). There were also no significant differences in occurrence of aggression towards novel opposite-sex individuals between paired and unpaired individuals (Chi-square test: $\chi_1^2 = 0.000$, $p = 0.999$).

Table 3.
Descriptive statistics for aggression in male and female zebra finches.

Sex	N	Same-sex aggression		Opposite-sex aggression	
		Latency (s)	Duration (s)	Observed	Not observed
Females	24	175.4 ± 140.6	2.4 ± 4.3	13	11
Males	24	128.0 ± 128.4	3.4 ± 4.7	7	17

Values are means ± SD. Data are displayed for both aggression contexts: mate-competition aggression (against a same-sex intruder) and aggression when first introduced to an opposite-sex potential pair partner.

3.3. Social preference

There were no significant differences between males and females in terms of the proportion of time spent near novel conspecifics in the social preference test (Wilcoxon rank sum test: $W = 310$, $N_1 = 21$, $N_2 = 20$, $p = 0.657$) (Table 4). When males and females were pooled together, we found that birds preferred the familiar conspecifics to the novel conspecifics (Chi-square test: $\chi_1^2 = 5.49$, $p = 0.02$). However, there was no significant difference between birds that eventually paired and those that remained unpaired in terms of the proportion of time spent near novel conspecifics (Wilcoxon rank sum test: $W = 174$, $N_1 = 30$, $N_2 = 11$, $p = 0.323$; Figure A6 in the Appendix).

3.4. Correlations between traits

There were no significant correlations between the traits measured (exploration, aggression, and social preference; Pearson's correlations, all p values > 0.30).

Table 4.
Descriptive statistics for social preferences in male and female zebra finches.

Sex	N	% Near novel	Individuals that preferred familiar	Individuals that preferred novel
Females	21	33.5 ± 32.3	15	6
Males	20	29.6 ± 29.4	14	6

Data reflect the percentage of time that individuals elected to spend near the novel birds, rather than the familiar birds. Values are means ± SD unless otherwise indicated.
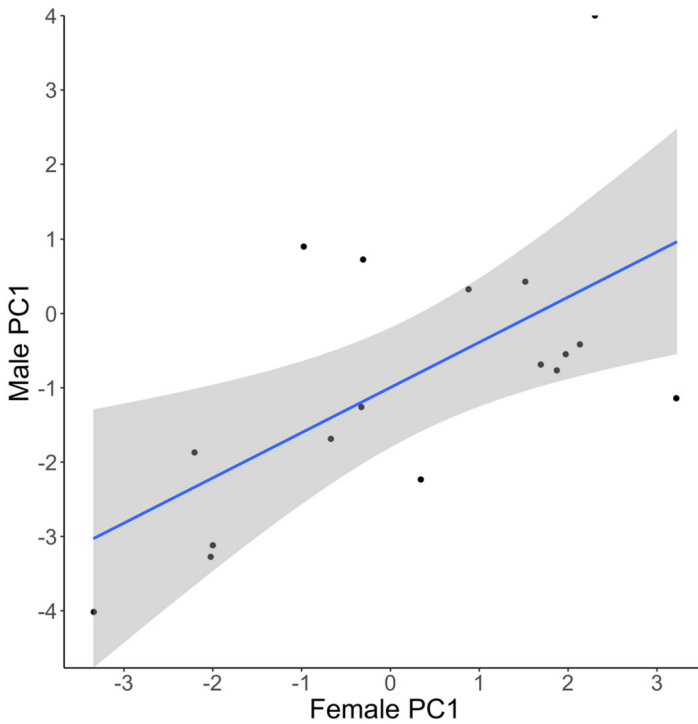
Figure 5. Birds select mates that are similar to them in exploration. Males and females within a pair were significantly correlated on PC1 scores. Shading represents 95% confidence interval.

3.5. Assortative mating

Consistent with previous studies, not all zebra finches paired despite ample opportunities to do so. By the end of the study, 70% of birds had paired (cf., 64%; Griffith et al., 2017), for a total of 16 pairs.

We found evidence that pairing is influenced by exploration, with birds selecting pair partners of similar exploration scores on PC1 (Pearson's correlation: $r = 0.614$, $N = 16$, adjusted $p = 0.044$; Figure 5). There was no evidence of assortative mating on any of the other variables: not by exploration PC2 (Pearson's correlation: $r = 0.232$, $N = 16$, adjusted $p = 0.618$), latency to aggression (Spearman correlation: $r_s = -0.394$, $N = 16$, adjusted $p = 0.294$) or duration of aggression (Spearman correlation: $r_s = 0.017$, $N = 16$, adjusted $p = 0.949$), nor by social preference for novel or familiar conspecifics (Spearman correlation: $r_s = -0.079$, $N = 16$, adjusted $p = 0.949$). Of the pairs, there was substantial variability in latency to pair formation,
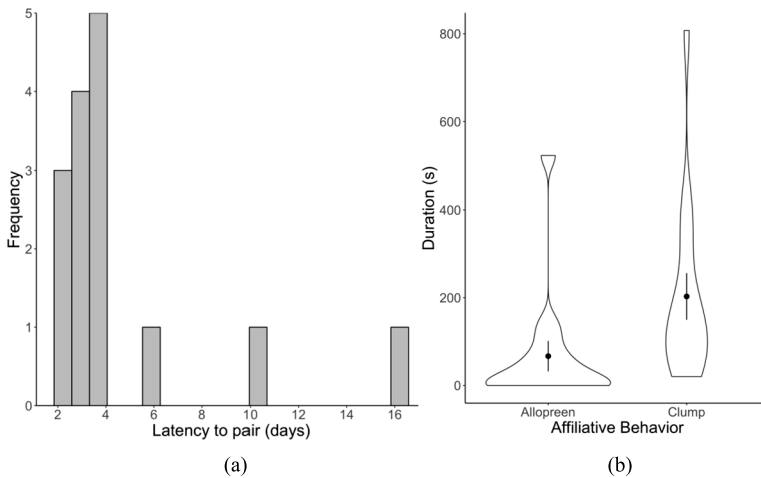
Figure 6. Pair bond formation and affiliative behaviours. Pairs exhibited variation in (a) latency to pair bond, as well as (b) duration of affiliative behaviours (i.e., allopreening and clumping) prior to pair bond formation.

with pairs forming as quickly as two days, or as late as 16 days (Figure 6a), as well as variation in the amount of affiliative behaviours observed prior to pair formation (Figure 6b). However, amount of affiliative behaviour was not influenced by pair similarity in exploration (Spearman correlations, all p values > 0.44). And, while birds sampled multiple potential mates, the number of non-pair partners that individuals interacted with was not predicted by their personality traits (Pearson's correlation, all adjusted p values > 0.97).

Next, we assessed whether the similarity in pair partners predicted their latency to pair. That is, do more similar birds pair faster? Pair partner similarity was assessed using the absolute value of the pair difference in PC score. However, similarity in exploration did not predict latency to pair, either for PC1 ($r = 0.25$, $N = 14$, $p = 0.37$) or PC2 ($r = -0.34$, $N = 14$, $p = 0.22$) (Figure A7 in the Appendix). Exploration score also did not influence latency to pair for females (PC1: Spearman correlation: $r_s = -0.096$, $N = 14$, $p = 0.294$; PC2: Spearman correlation: $r_s = 0.064$, $N = 14$, $p = 0.822$) or males (PC1: Spearman correlation: $r_s = -0.071$, $N = 14$, $p = 0.803$; PC2: Spearman correlation: $r_s = -0.164$, $N = 14$, $p = 0.558$). Thus, high explorers did not pair faster than low explorers.

4. Discussion

We found that assortative mating may occur by personality, specifically by the trait of exploration, in zebra finches. Birds used a relative trait strategy, in which absolute levels of a trait were not as important as the match between the pair: individuals did not prefer high or low explorers overall, but chose mates that were similar to them in exploration. Birds exhibited consistent individual differences in their exploration of a novel environment. This result ($R = 0.489$, 95% CI: [0.264, 0.698]) is comparable to, though lower than, previous estimates of repeatability of exploration in this species ($R = 0.76$, 95% CI: [0.46, 0.92]; David et al., 2012b). In our principal component analysis that reduced the number of exploration variables, we found that females scored higher on PC1 (fewer novel components, fewer novel features, longer latency to visit the first novel component) than males. However, more similar individuals did not pair faster. Aggression and social affiliation preferences were not relevant to zebra finch mate choice.

Our exploration tests were conducted in a non-social context, similar to Schuett et al. (2011b), who found that when pairs were assigned mates with similar exploration scores, they had improved reproductive outcomes. Our findings that exploration influences pairing align with their results. However, previous studies have not found evidence of assortative or disassortative mating by exploration in this species; specifically, our results differ from those of McCowan et al. (2014). These contrasting findings might stem from the methods used to assess exploration. Schuett et al. (2011b) measured exploration in a non-social context, with the individuals isolated, while McCowan et al. (2014) measured exploration with individuals tested in a group context. Exploratory behaviour, however, varies between social and non-social contexts, as other individuals can influence the focal bird's behaviour. Females are particularly susceptible to decreased consistency between social and non-social contexts (Schuett & Dall, 2009; Mainwaring et al., 2011). Therefore, our results are not inconsistent with previous findings, when accounting for differences in methodology.

On a proximate level, behaving in similar ways to another individual, or performing the same behaviour synchronously, has been linked to increases in affiliation. Observational studies in cetaceans indicate that synchronized behaviours (e.g., swimming, surfacing, body contact) are indicators of affiliation and alliance (Connor et al., 2006; Senigaglia et al., 2012). A manipulation of behavioural synchrony and affiliation in humans revealed that

participants who tapped their fingers in synchrony with an experimenter rated them as more likeable than experimenters that tapped asynchronously (Hove & Risen, 2009). In addition, female rainbow krib prefer males that behave predictably (Scherer et al., 2018). Thus, a combination of factors — both reward from predicting a pair partner's behaviour, and increased affiliation from behaving in similar ways as the pair partner — might provide the proximal basis of a pair bond. Over time, increased familiarity with a partner can also increase behavioural synchrony (Prior et al., 2019).

Such a preference for individuals with similar personality traits could occur because individuals find predictable interactions rewarding. Reward, and reward prediction error, are driven by mesolimbic dopaminergic neurons (Schultz et al., 1997). Similar circuitry is involved in pair formation: newly paired zebra finches (though not unpaired, courting birds) exhibited increased dopamine levels in the medial striatum (Banerjee et al., 2013). Courtship behaviours (e.g., song) have been linked to dopamine expression in midbrain central grey, with caudal ventral tegmental area dopaminergic neurons involved in social motivation more broadly (Goodson et al., 2009).

On an ultimate level, it might be adaptive to seek out mates with similar behaviour to coordinate parental care duties, such as nest building, incubation, and provisioning. Assortative mating by personality trait may be favoured in species where biparental care is required to raise the young, as this could allow for increased parental coordination of offspring care. Even before eggs are laid, similarity of exploration within pairs might lead to increases in reproductive success through a decrease in the latency to commence reproductive efforts (Gabriel & Black, 2011), or pair compatibility might result in an increase in copulation frequency (Spoon et al., 2007) and success. However, to our knowledge, the influence of adult personality traits, and pair similarity, on latency to nest construction — or nest site location — in zebra finches has not yet been examined. A current study is underway in our lab investigating the relationship between pair similarity and latency to nest initiation. Once the eggs are laid, parents must cooperate to care for the offspring. Zebra finches, as a socially monogamous species with biparental care, rely heavily on both parents to raise the altricial offspring. The consequences of selecting a mate that is not behaviourally compatible have been elucidated by previous work on the fitness benefits of mate choice in chosen vs. assigned pairs (Ihle et al., 2015). In brief, assigned pairs of zebra finches behave less synchronously, decrease nest attendance around hatching, and

have lower reproductive success than pairs that were allowed to choose their mates. Assortative mating by personality traits affects reproductive success in other avian species. Pairs that are more similar in exploration are more likely to have offspring survive to fledging (Gabriel & Black, 2011) and have offspring in better condition at fledging (Both et al., 2005). Thus, there are indications that pairing assortatively by personality trait, such as exploration, leads to increased behavioural compatibility of the pair, and thereby results in increased reproductive success.

Suggestions of sex differences in exploration have previously been found in zebra finches. While the magnitude of exploratory behaviour does not appear to differ between males and females (Martins et al., 2007; Schuett & Dall, 2009; Mainwaring & Hartley, 2013), the consistency (or repeatability) of exploration has conflicting findings. Females were inconsistent or less consistent in exploration, as compared to males (Schuett & Dall, 2009; Wuerz & Kruger 2015), though others have reported that females are consistent in exploration between two and nine months of age (David et al., 2012b). Our measure, however, incorporated both amount of exploration and latency to explore, whereas previous studies measured these separately; only amount of exploration (e.g., Schuett & Dall, 2009; Mainwaring & Hartley, 2013) or latency to visit all novel feeders within the exploration test (Martins et al., 2007). Our combined measure may provide more nuanced insight into variation in exploratory behaviour.

By contrast, aggression and social preference did not appear relevant to mate choice. The lack of significant results for aggression, in particular, is intriguing given previous findings that linked a 'proactive' behavioural syndrome encompassing exploration, activity, neophobia, and reaction to a startle test with increased social dominance in a food-competition context (David et al., 2011). Our results are perhaps less surprising in the context of previous findings that, while females will indicate a preference for more or less aggressive males at a given time, their choice has low consistency (Forstmeier & Birkhead, 2004). Moreover, we saw a relatively low amount of aggression overall (less than 20 sec of aggression from the most aggressive individuals). As this species is not generally aggressive, nor are clear dominance hierarchies visible in the wild (Zann, 1996), the variability present in aggressive tendencies may be too low to serve as a means of selection or provide a useful indication of mate quality. Together, this suggests that

aggression is not a highly relevant trait for individual mate choice, though it may influence reproductive success post-pairing.

Preference for novel or familiar conspecifics is less well researched, but has previously been used to index social competence (Kelly & Goodson, 2014), and was of interest because it might also indicate some degree of preference for familiarity or predictability, which could influence latency to pair. While individuals generally demonstrated strong preferences, pairs did not assort based on social preference. This might be due to the fact that all potential mates were equally novel, having been introduced at the same time, or because preference for familiar same-sex conspecifics does not carry over for opposite-sex individuals.

Possible limitations of our study include the fact that aggression and social preference were only measured at one time point to minimize any association with prior experiences in the testing apparatus that might influence behaviour at test (e.g., aggressive behaviour stemming from a past aggressive encounter). Thus we cannot draw any conclusions as to their stability over time, and some definitions of personality traits would exclude our measurements (e.g., Sih & Bell, 2008; though cf., Kelly & Goodson, 2014). Another caveat is that our aggression test used live conspecific competitors to induce aggression rather than a mirror. While using conspecifics introduces variation (i.e., perhaps the aggression of the focal individual was influenced by that of the competitor, rather than deriving from their own trait of aggression), the alternative mirror test poses its own set of issues. Animals may differ physiologically and behaviourally in their reaction to a mirror as opposed to a live conspecific (Balzarini et al., 2014). Moreover, dominance interactions with live conspecifics have been shown to be repeatable over time (David et al., 2011). Overall, it is unclear what ecological relevance a mirror test might hold, in relation to our mate-competition aggression paradigm, which explicitly tests aggression in a mating context (though see Schuett et al., 2011).

Given the design of our study, which studied pair formation in a group setting, it is possible — and even likely — that individuals did not pair with their most ideal mate. We do not view this as a detriment, however, but as the goal of our design, as our study provides detailed insight into the reality of zebra finch mate choice in flocks. Under conditions of competition, with limited time and energy to invest in interacting with a pool of potential mates (Rosenthal, 2017), individuals still appeared to achieve assortative mating

via exploration. One alternative possibility is that high exploring individuals were favoured as mates, leaving the leftover low explorers to form pairs, and thus providing a semblance of assortative mating. However, we view this scenario as unlikely given that there was no relationship between an individual's exploration score and their latency to pair — that is, there were no 'leftover' low exploring birds. We also acknowledge that mate choice could have been based on other factors correlated to exploration, such as body size, and encourage future studies to investigate these factors. For example, adults in poor body condition display increased motivation to explore (Crino et al., 2017). However, personality exerts effects on exploration independent of body condition (David et al., 2012a), and birds in the current study were allowed ad libitum access to food before the personality tests took place.

In conclusion, we found that zebra finches select mates that are similar to them in exploration. Importantly, our experiment used a context in which zebra finches could choose from a variety of potential mates that varied in multiple traits, and followed individuals throughout the full courtship period. Our results validate and expand upon the findings of more commonly used mate choice paradigms, such as multi-choice chamber paradigms, which found that zebra finches may assort by exploration. Assortative mating by personality may allow for increased behavioural compatibility of a pair, benefitting later reproductive success.

A challenge for the field is to determine how personality traits are transduced into specific sets of behavioural cues that are present during courtship. How are personality traits detected by conspecifics during courtship, and are personality traits weighted equally by both sexes when selecting a mate? What behavioural cues are reliable indicators of exploration? Do dynamic behavioural traits such as personality outweigh static morphological cues? Such a question could be tested through manipulating external appearance (e.g., through artificially altering beak redness (Simons & Verhulst, 2011) or changing band colour (Burley et al., 1982)) between preference tests, to titrate out the relative importance of personality from physical traits in mate choice. Answers to these questions will yield an improved understanding of the importance of gathering and evaluating dynamic social information during courtship.

Acknowledgements

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Appendix: Principal component analysis on exploration

We conducted a principal component analysis on the six exploration variables (number of novel components and features, number of repeat components and features, latency to visit the first novel component and feature). All variables were averaged over the two novel environment tests conducted.
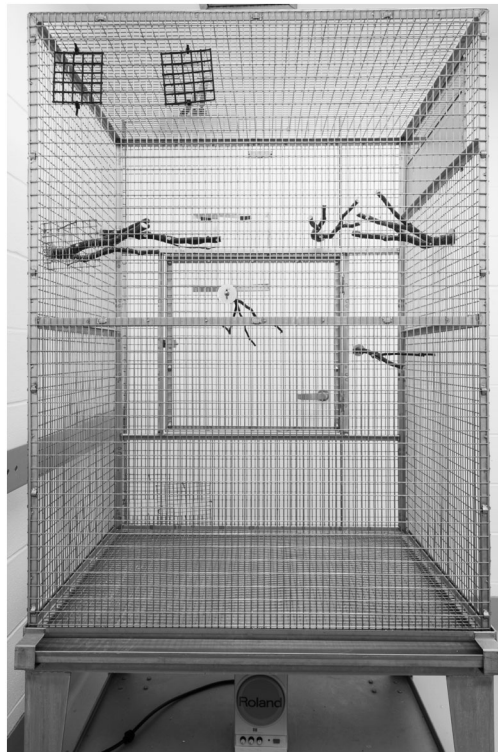

Figure A1. The novel environment apparatus. This aviary contained two different kinds of unique perches, three of each. Birds were visually and acoustically isolated from conspecifics, except for a speaker placed at the centre of the base of the novel environment aviary, which played pre-recorded aviary noise. Each perch was considered a feature, and each branch of the perch was labelled a component. Birds were scored for their latency to visit novel features and component, as well as for the total number of features and components visited during a 5 min span.
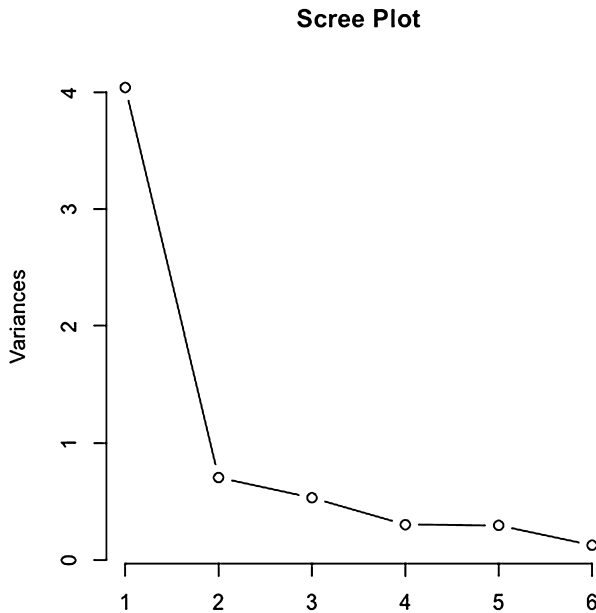
Scree Plot

Figure A2. Scree plot of variance explained by the principal component analysis. As a sharp drop in explained variance was observed after the second principal component, only the first two (PC1 and PC2) were retained for further analysis.

A Bartlett's test of sphericity (calculated using the 'REdaS' package in R; Maier, 2015) confirmed that there was sufficient shared correlation between the variables to merit using a principal component analysis to reduce the dimensionality of the data ($\chi^2_{15} = 108.289$, $p < 0.001$). We next examined a scree plot in order to determine how many principal components to retain (Figure A2). From visual inspection, the first two principal components were retained, explaining 79.1% of the variance in the data (PC1 = 67.3%, PC2 = 11.8%). We then assessed the loadings of the variables on the retained principal components (Table 4).
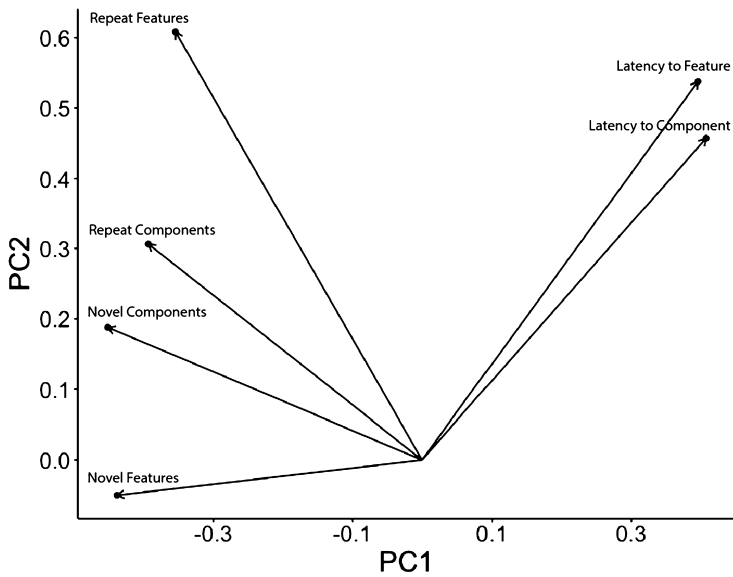
Figure A3. Principal components loading plot for PC1 and PC2. As can be observed, the latencies to visit novel features and components were related, as were the number of novel and repeat components visited.
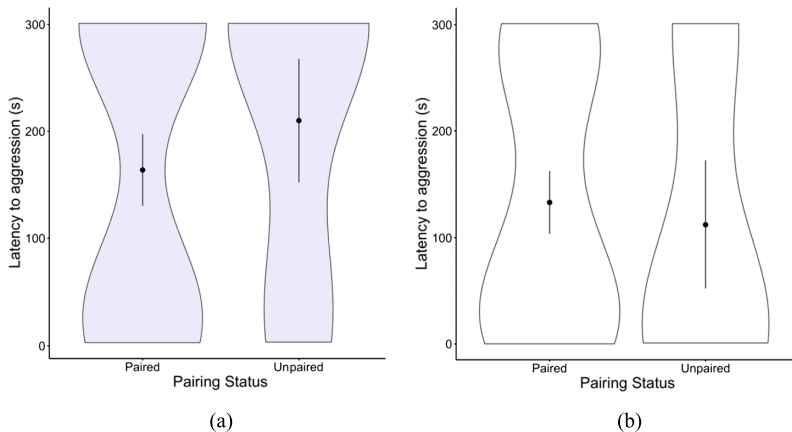

Figure A4. Paired and unpaired birds do not differ in latency to aggression. Data are drawn from the mate-competition aggression test, for the latency to display aggression towards a same-sex competitor. Violin plots for (a) females (lavender) and (b) males (white), overlaid with mean $+/-$ one standard error.

(a)   (b)
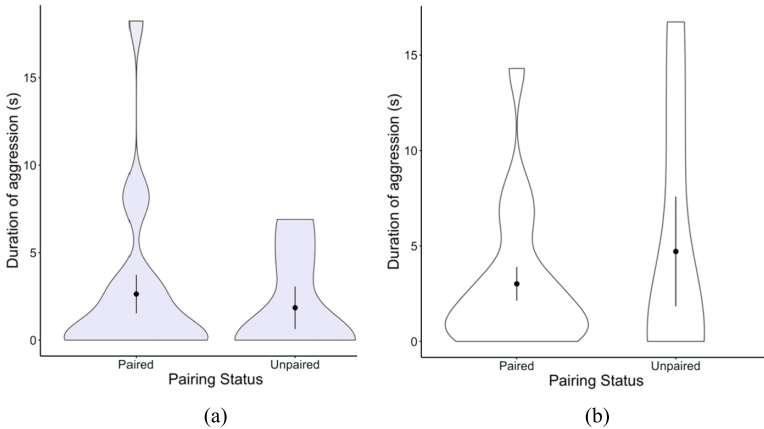
Figure A5. Paired and unpaired birds do not differ in duration of aggression. Data are drawn from the mate-competition aggression test, for the duration of aggression displayed towards a same-sex competitor. Violin plots for (a) females (lavender) and (b) males (white), overlaid with mean $+/-$ one standard error.

(a)   (b)
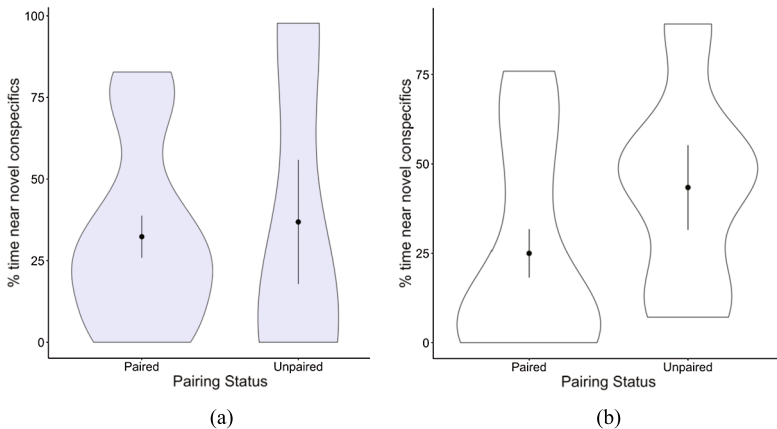
Figure A6. Paired and unpaired birds do not differ in social preference. Data drawn from the social preference test, where individuals could indicate a preference for familiar or novel same-sex individuals due to the proportion of time they spent in proximity. Violin plots for (a) females (lavender) and (b) males (white), overlaid with mean $+/-$ one standard error.

(a)   (b)
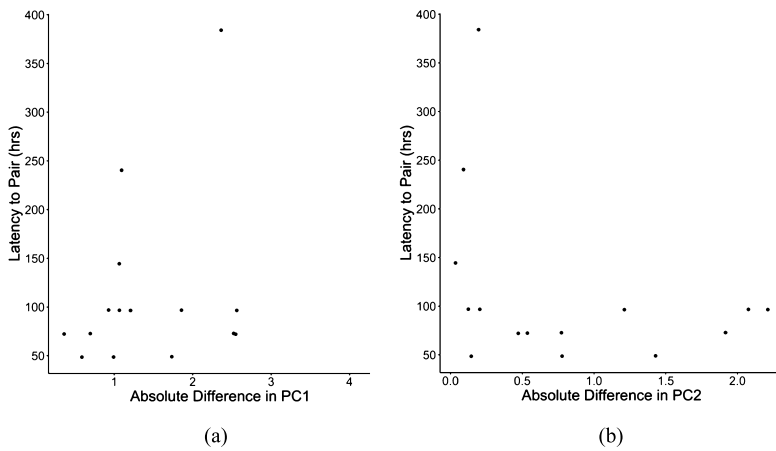
Figure A7. Difference in exploration does not predict latency to pair. Difference in exploration scores calculated from the absolute value of the difference between males and females within a pair in terms of their score on each of the principal components, (a) PC1 and (b) PC2.