



Personality affects zebra finch feeding success in a producer–scrounger game

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Recent evidence strongly suggests that natural selection can favour the evolution of consistent individual differences in behaviour ('personalities'). Indeed, personality shows heritable variation and has been linked to fitness in many species. However, the fitness effects of personality are highly variable within and between species. Furthermore, the nature of the causal influence of personality on an organism's fitness remains unclear so far. Competition has been proposed as a factor modulating this relationship. Thus, personality has been found to affect individual success in competition by interference in a few species, but its influence in scramble competition remains unexplored. We assessed exploratory tendencies (thought to be a key component of personality) in a model species, the zebra finch, *Taeniopygia guttata*. In a first session, we formed foraging flocks composed of four individuals with different exploration scores, and allowed them to play producer–scrounger games repeatedly. During a second session, individuals were reassigned to different flocks to check for consistency in the influence of exploratory tendency across different social contexts. Exploratory tendency influenced individual feeding success during the first session but not during the second one. High-exploratory birds were less successful at finding food (i.e. playing the producer tactic) and consequently had a lower feeding success, but were presumably able to adjust their behaviour between sessions. We discuss our results in relation to the interactive effects of both personality and experience, and highlight the role of competition processes on the evolution of personality.

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Consistent behavioural differences between individuals and across situations (so-called 'personalities') have recently become of prime interest to behavioural ecologists (Réale et al. 2007). Increasing evidence for animal personality raises the question of the factors at play in the maintenance of behavioural variation within populations (Sih et al. 2004). To address this issue from an adaptive perspective, behavioural ecologists investigate the extent to which personality traits such as boldness, exploratory tendencies or risk-taking behaviour can evolve through natural selection (Quinn et al. 2009). Consistent behavioural variation has been described in a large range of species, from molluscs (Sinn et al. 2006) to arthropods (Johnson & Sih 2007) and vertebrates (David et al. 2011). Personality traits also show substantial levels of additive genetic variation (Drent et al. 2003) and can have important consequences for fitness (Smith & Blumstein 2008). For instance,

activity levels have been negatively related to survival in female red squirrels, *Tamiasciurus hudsonicus* (Boon et al. 2008).

The impact of personality on fitness has mainly been studied through its influence on reproductive success and survival (Smith & Blumstein 2008). However, the mechanisms responsible for these effects lack experimental attention and as a result remain largely unknown. In the great tit, *Parus major*, at least, exploratory tendencies predict differential survival across years and between the sexes, and competition for food in the winter and for territories in the spring could explain these fluctuating pressures on personality (Dingemanse et al. 2004). Although foraging behaviour has already been related to fitness in several species (Ritchie 1990; Blanckenhorn 1991; Lemon 1991), direct evidence of an influence of personality on the outcome of foraging competition is rare (but see Fox et al. 2009; David et al. 2011).

Foraging competition can be divided into two separate types. In interference competition, competitors physically interact to acquire specific food items. In scramble competition, they exploit the resource without physically interacting. Individual success in both types of competition generally involves different abilities, such as dominance over conspecifics or a better capacity to detect cryptic food items. This explains why both types are traditionally

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investigated separately. Personality has been found to influence the likelihood of becoming dominant during interference competition for food in the mountain chickadee, *Poecile gambeli* (Fox et al. 2009), in the zebra finch, *Taeniopygia guttata* (David et al. 2011), and in the three-spined stickleback, *Gasterosteus aculeatus* (Ward et al. 2004). To date, however, few studies have examined the effect of personality on the outcome of scramble competition (Beauchamp 2001). For instance, shy barnacle geese, *Branta leucopsis*, preferentially use social information when feeding in groups (Kurvers et al. 2010) and therefore are more likely to exploit the discoveries of group mates. As the two types of foraging competition involve different abilities, individuals that are successful in interference competition may not necessarily be successful in scramble competition. This could lead the two types of competition to exert contrasting selection pressures on the evolution of personality.

In the present study, we addressed this issue by investigating the behaviour of individuals varying in personality types while engaged in a producer–scrounger foraging game (Barnard & Sibly 1981; Giraldeau & Caraco 2000). In this system, individuals forage in a group and allocate their sampling effort between searching for their own food (the producer tactic) and exploiting flockmates' discoveries (the scrounger tactic). This foraging game enabled us to investigate the influence of personality on the use of both personal and social information associated with alternative foraging tactics, and the resulting payoffs leading to fitness consequences in scramble competition. We first formed foraging flocks composed of individuals with different exploratory tendencies. Then we recorded their feeding success and their use of both producer and scrounger foraging tactics across repeated trials. Birds were tested in two different flocks with different flockmates to assess both the consistency of exploration tendency on foraging behaviours and its flexibility (Briffa et al. 2008; Dingemanse et al. 2010). We chose the zebra finch as our model organism as it has already been successfully used in studies of personality (Schuett & Dall 2009; David et al. 2011) and social foraging (Beauchamp 2006).

METHODS

Study Subjects

Zebra finches are small Australian passerine birds living and feeding in large colonies, from 10 to hundreds of individuals, in the wild (Zann 1996). Feeding flocks are formed either by individuals joining others already feeding on the ground or by individuals landing on the ground in a cohesive flock (Zann 1996). These feeding habits indicate that zebra finches can rely on flockmates' behaviour to locate food patches and thus attempt to scrounge from their discoveries. We purchased 15 male and 15 female zebra finches, all between 2 and 3 months old, from a local supplier (L'oisellerie de l'Estrie, Québec). Before the experiments, birds were kept in three adjacent rooms in same-sex groups of two to three individuals in small home cages (29 × 52 cm and 38 cm high) containing four feeders and four perches. Room temperature was maintained at 24 ± 1 °C on a 12:12 h light cycle (0800–2000 hours EDST). Millet seeds, water and cuttlebones were provided ad libitum, while vegetables and an egg mixture were occasionally offered. Each individual wore a numbered orange plastic leg ring (AC Hughes, Hampton Hill, U.K.; size XF) allowing individual identification. After the experiment, birds were kept in groups of two to be used in subsequent studies. All procedures applied to animals in this study complied with guidelines from the Canadian Council for Animal Care and were approved under protocol 0210-676-0211 of the UQAM committee for animal care.

Assessment of Exploratory Tendencies

Following previous studies of birds' exploratory behaviour (Dingemanse et al. 2002; David et al. 2011), we assessed individual exploratory tendencies twice with a 1 week interval in a large cage (the exploration apparatus, 120 × 120 cm and 60 cm high) with which the birds were unfamiliar (Réale et al. 2007). This cage had opaque walls, a wire-mesh ceiling and contained five artificial trees each with four small branches. Birds were deprived of food for 1 h to control for feeding motivation before being introduced singly in a black box placed against a small sliding door on one side of the apparatus. The experimenter (M.D.) then gently opened the door with a pulley system from outside the room, which successfully motivated birds to enter the apparatus. Individual behaviour inside the apparatus was recorded for 1 h on a video camera (Sony HDR XR500) placed 1 m above it. During the analysis, the experimenter recorded the number of movements between trees and between each branch of a single tree. Each movement was easily identifiable through a short flight between two perches. Birds did not perform any other jumps or lateral movements on the same perch. Following this experiment, individuals were sorted into four categories as a function of the cumulative number of movements they performed within the apparatus, averaged across the two trials. Zebra finches generally show a highly consistent behaviour in the apparatus during 30 or 60 min trials (M. David, unpublished data), suggesting that individual behaviour during exploration trials is not the mere result of reaction to stress or attempts to escape and reliably represent an intrinsic tendency to move around in an unfamiliar environment. Birds in the upper-third, middle-third and lower-third of the distribution were respectively considered as high-, medium- and low-exploratory individuals, irrespective of sex. As six of the tested birds (three males and three females) did not come out of the small black box, they constituted a fourth category (NA) of individuals that had no quantitative exploratory score but were still used in the subsequent parts of the experiment.

Producer–Scrounger Game

Foraging experiments started 1 week after the last exploration trial. Each flock was composed of one randomly chosen individual from each of the four exploration categories. We did not associate birds that had previously been housed together, to avoid any potential effect of familiarity. We also decided to separate the males and females into same-sex foraging flocks to avoid any interference from intrasexual competition or male courtship.

Foraging experiments were divided into two similar sessions lasting 3 days each (sessions A and B). On the first day of a session, individuals were given a unique combination of blue and light blue leg rings for identification from the video footage. Thus, in addition to their orange identification leg ring, the four birds in each flock wore one of the following colour combinations: light blue–light blue, light blue–blue, blue–light blue, blue–blue. We chose this colour as it has no effect on sexual or agonistic interindividual interactions (Burley et al. 1982; David et al. 2011). Ring colour combination had no effect on any recorded variables ($P > 0.10$ for all tests). Each bird was then placed with its flockmates inside a large aviary (1.5 × 3.8 cm and 2.3 m high) containing two tables (1.4 × 0.7 m), which supported a foraging grid with 64 small wells (1.6 in diameter and 1 cm deep) every 8.1 cm. Two large perches and two water containers were placed on one table. The aviaries were on the same light cycle and at the same temperature as the rooms in which the birds were previously held. To help familiarize the birds with the aviary and the foraging grid, each well was filled with millet seeds on the first day.

On the second day, the grid and the aviary floor were cleaned in the morning to prevent birds from feeding on seeds left on the floor.

Birds were then deprived of food for 1 h before training trials. Then, each flock was given five white millet seeds per well in 10 wells every hour for 7 h, enabling them to forage in flocks during seven training trials. Wells to be filled were randomly chosen for each trial. Each flock was given seeds ad libitum in all grid wells for the rest of the second day. The same procedure was performed again on the third day (test phase) except that each flock underwent five experimental trials that were videorecorded and used for analysis. Afterwards, individuals were returned to their home cages in groups of two to three individuals per cage and given seeds and water ad libitum.

Birds were allowed to rest for 4 days before undergoing the same procedures but with different flockmates.

Sample Sizes

We tested six flocks (three per sex) of four birds per session. Twenty-four birds were thus used during session A. To test behavioural consistency across flocks, we reused 18 of these birds during session B. Because of our experimental design (four different birds in three same-sex flocks), it was impossible to form three same-sex flocks in session B with a different composition from that in session A. That is why we reused only 18 birds and introduced six new birds (three males and three females, four coming from the low-exploration category, one from the medium-exploration category and one from the high-exploration category) in session B. In session B, birds were also randomly associated with flockmates with which they had never interacted before. However, owing to a lack of available individuals, two birds were tested together in the same flock in both sessions. Removing these individuals from the analyses does not substantially change the results.

To sum up, within-session tests were performed on 24 individuals (six flocks of four individuals), whereas between-session tests were performed on 18 birds.

Data Analysis

During video analysis, we recorded the arrival rank on the grid so that the bird landing first obtained the score 1. The last bird to land obtained the score 4. We recorded the individual number of producing events, corresponding to a bird finding a hitherto undiscovered well containing seeds, and the number of seeds eaten ('produced'). We recorded the individual number of scrounging events, corresponding to a bird joining a well on which other birds were already feeding or had just left within a few seconds, and the number of seeds they scrounged. The variable 'number of seeds ingested' corresponded to the sum of both the number of seeds produced and scrounged over the five trials. 'Finder's share' was defined as the number of seeds eaten per producing event. As one bird ingested no seeds during session A, analyses involving the variable 'proportion of seeds scrounged' was performed with only 23 individuals.

Behavioural consistency was assessed between the two trials for exploration tendencies and between the five trials of a given session for foraging behaviours, by calculating the intraclass correlation coefficient (repeatability, R), using the method of Lessells & Boag (1987). A 95% confidence interval, CI, was also calculated for each coefficient (Nakagawa & Schielzeth 2010). As two individuals from the low-exploration category did not come out of the black box during one exploration trial, repeatability was calculated from only 22 individuals (the six individuals from the NA category were discarded from this analysis). Exploration tendency values were averaged from the two trials and foraging behavioural values were averaged from the five trials of a given session for each variable and used thereafter.

The number of individual foraging events (occurrence of producing and scrounging) was always strongly correlated with the

number of seeds eaten using each tactic within each session (Pearson correlations: session A: 'producing events' versus 'seeds produced': $r_{23} = 0.89$; 'scrounging events' versus 'seeds scrounged': $r_{23} = 0.96$; 'proportion of scrounging events' versus 'proportion of seeds scrounged': $r_{22} = 0.95$; session B: 'producing events' versus 'seeds produced': $r_{23} = 0.92$; 'scrounging events' versus 'seeds scrounged': $r_{23} = 0.96$; 'proportion of scrounging events' versus 'proportion of seeds scrounged': $r_{23} = 0.97$; $P < 0.0001$ for all tests). For conciseness we only report the analyses performed on the variables 'number of seeds produced', 'number of seeds scrounged' and 'number of seeds ingested'. Analyses conducted with the variable 'number of events' yielded the same results.

The influence of exploratory tendency on foraging behaviour was tested using nonparametric Friedman tests. This enabled us to control for the nonindependence of data within flocks, that is, to control for the possibility that the behaviour of a focal individual was influenced by flockmates. Paired t tests were used to check whether an individual's foraging behaviour differed significantly between the two sessions. The influence of exploratory tendency on between-session variation in individual foraging behaviour was tested using nonparametric Kruskal–Wallis tests. Only two birds from the low-exploration category were tested during both sessions (see Sample sizes above). We then excluded this category from the analyses based on between-session variation in behaviour to avoid any sample size effect, and only used the three other exploration categories (NA, medium and high).

The relationship between arrival rank on the grid and foraging behaviour was tested using Pearson correlations.

Variables were log or root transformed to reach normality when needed. Statistical analyses were performed with JMP 5.0.1 and Statview 5.0 software (SAS Institute Inc., Cary, NC, U.S.A.).

RESULTS

Exploratory Tendencies' Consistency

The number of movements performed within the exploration apparatus was highly consistent between the two trials ($R = 0.60$, 95% CI = 0.36–0.84, $F_{21,43} = 4.05$, $P = 0.001$, $N = 22$; Fig. 1) and did not differ between the sexes ($t_{22} = -0.46$, $P = 0.651$).

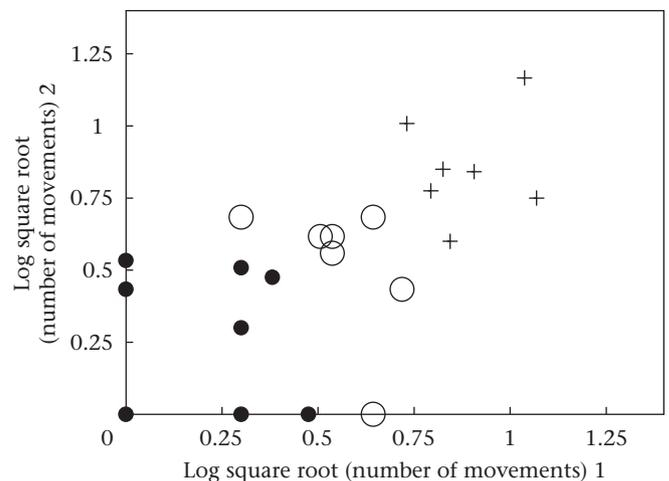


Figure 1. Relationship between the two individual exploration scores measured as the number of movements performed within the exploration apparatus. Birds were thereafter separated into four exploration categories: a high-exploratory category (+), a medium-exploratory category (○) and a low-exploratory one (●). The fourth category (NA) corresponded to the birds that never entered the exploration apparatus and stayed in the small black box.

Table 1
Within-session repeatability estimates and associated significance of the variables recorded during producer–scrounger trials

Measured variable	Session A				Session B			
	Males		Females		Males		Females	
	R (CI)	P	R (CI)	P	R (CI)	P	R (CI)	P
Arrival rank on the grid	0.07 (–0.18–0.32)	0.21	0.67 (0.42–0.92)	<0.001	0.53 (0.23–0.84)	<0.001	0.39 (0.06–0.71)	<0.001
Number of seeds produced	0.51 (0.19–0.82)	<0.001	0.65 (0.39–0.91)	<0.001	0.37 (0.04–0.70)	<0.001	0.58 (0.29–0.87)	<0.001
Number of seeds scrounged	0.49 (0.17–0.81)	<0.001	0.59 (0.30–0.87)	<0.001	0.45 (0.12–0.77)	<0.001	0.71 (0.48–0.94)	<0.001
Proportion of seeds scrounged	0.16 (–0.17–0.49)	<0.001	0.68 (0.43–0.93)	<0.001	0.33 (0.05–0.75)	<0.01	0.56 (0.26–0.86)	<0.001
Number of seeds ingested	0.60 (0.31–0.89)	<0.001	0.64 (0.37–0.91)	<0.001	0.28 (–0.04–0.59)	<0.01	0.56 (0.26–0.85)	<0.001
Finder's share	0.10 (–0.23–0.54)	<0.001	0.48 (0.15–0.80)	<0.001	0.09 (–0.18–0.35)	0.18	0.17 (–0.13–0.46)	0.06

Values in parentheses correspond to the coefficient's 95% confidence interval (CI).

Foraging Behaviour Consistency Within and Between Sessions

Mean number of seeds produced per trial was 8.9 ± 2.6 (mean \pm 95% CI) in session A and 8.7 ± 1.8 in session B. Mean number of seeds scrounged per trial was 2.1 ± 0.9 in session A and 2.4 ± 1.1 in session B. Mean finder's share was 2.2 ± 0.3 seeds in session A and 2.8 ± 0.2 seeds in session B. Arrival rank, number of seeds produced, scrounged, ingested and finder's share were significantly repeatable across trials in females within each session (Table 1). In males, the size of the finder's share was not repeatable, while arrival rank and proportion of seeds scrounged were not repeatable only during session A (Table 1). Males and females differed significantly in arrival rank consistency in session A, as the confidence intervals do not overlap. No other repeatability estimate differed significantly between the sexes. Between sessions, no variable was found to be significantly repeatable, except female arrival rank (Table 2).

Effects of Exploratory Tendency on Foraging Tactic Use

Arrival rank on the grid was not affected by exploratory tendency (session A: $\chi^2_3 = 1.40$, $P = 0.71$; session B: $\chi^2_3 = 0.75$, $P = 0.86$). In both sessions A and B, exploratory tendencies were not linked to the number of seeds scrounged (session A: $\chi^2_3 = 2.53$, $P = 0.47$; session B: $\chi^2_3 = 1.60$, $P = 0.66$) or the proportion of seeds scrounged (session A: $\chi^2_3 = 0.36$, $P = 0.95$; session B: $\chi^2_3 = 2.00$, $P = 0.57$). However, the number of seeds produced ($\chi^2_3 = 9.00$, $P = 0.03$), the total number of seeds ingested ($\chi^2_3 = 9.60$, $P = 0.02$) and to some extent the finder's share ($\chi^2_3 = 7.32$, $P = 0.06$) were all associated with exploration tendencies in session A (Fig. 2a,c), but surprisingly not in session B (seeds produced: $\chi^2_3 = 1.17$, $P = 0.76$; seeds ingested: $\chi^2_3 = 2.60$, $P = 0.46$; finder's share: $\chi^2_3 = 6.20$, $P = 0.10$; Fig. 2b,d). Specifically, high-exploratory individuals had a lower feeding success, produced less and had a lower finder's share than individuals from the other exploration categories in session A. The

Table 2
Between-session repeatability estimates and associated significance of the variables recorded during producer–scrounger trials

Measured variable	Males		Females	
	R (CI)	P	R (CI)	P
Arrival rank on the grid	0.28 (–0.45–1.01)	0.21	0.61 (0.12–1.11)	0.02
Number of seeds produced	–0.05 (–0.84–0.74)	0.55	0.22 (–0.53–0.98)	0.26
Number of seeds scrounged	0.48 (–0.14–1.09)	0.07	0.36 (–0.33–1.05)	0.14
Proportion of seeds scrounged	0.47 (–0.14–1.09)	0.07	0.37 (–0.31–1.05)	0.13
Number of seeds ingested	0.16 (–0.61–0.94)	0.32	0.36 (–0.34–1.05)	0.14
Finder's share	–0.14 (–0.92–0.64)	0.65	–0.21 (–0.97–0.54)	0.72

Values in parentheses correspond to the coefficient's 95% confidence interval (CI).

total number of seeds ingested by all individuals did not differ significantly between the two sessions ($t_{17} = -0.56$, $P = 0.58$).

The analyses linking feeding success, variation in foraging tactic use between sessions and exploratory tendency are summarized in Table 3. High-exploratory individuals showed a significant increase in the total number of seeds ingested between sessions A and B (Fig. 3a, Table 3). This increase was due to a higher number of seeds produced (Fig. 3b, Table 3) and a higher finder's share in session B compared to session A (Table 3). The number of seeds scrounged and the proportion of seeds scrounged did not increase between the two sessions. Both medium-exploratory individuals and birds from the NA category showed a significant decrease in the total number of seeds ingested between sessions A and B. This decrease was due to a lower number of seeds produced in session B compared to session A. As for high-exploratory birds, the number of seeds scrounged and the proportion of seeds scrounged did not vary between sessions. Therefore, between-session variation in the number of seeds ingested ($H_2 = 9.63$, $P = 0.01$) and the number of seeds produced ($H_2 = 7.89$, $P = 0.02$) differed between exploration categories. However, the variation in the number of seeds scrounged ($H_2 = 1.54$, $P = 0.46$), the proportion of seeds scrounged ($H_2 = 1.22$, $P = 0.54$) and the finder's share ($H_2 = 4.13$, $P = 0.13$) did not.

Finally, foraging tactic use was related to arrival rank on the grid both in session A (number of seeds produced: $r_{23} = -0.44$, $P = 0.03$; number of seeds scrounged: $r_{23} = 0.35$, $P = 0.10$; proportion of seeds scrounged: $r_{22} = 0.49$, $P = 0.02$) and in session B (number of seeds produced: $r_{23} = -0.56$, $P = 0.01$; Fig. 4a; number of seeds scrounged: $r_{23} = 0.34$, $P = 0.10$; Fig. 4b; proportion of seeds scrounged: $r_{23} = 0.51$, $P = 0.01$; Fig. 4c). Moreover, feeding success was marginally related to arrival rank in session A ($r_{23} = -0.38$, $P = 0.07$) and significantly related in session B ($r_{23} = -0.46$, $P = 0.03$; Fig. 4d). Birds that were the first to land on the grid preferentially used the producer tactic and had a higher feeding success. Birds among the last to land preferentially used the scrounger tactic and had a lower success.

DISCUSSION

Our results reveal that both exploration tendencies and foraging behaviours were repeatable within sessions, suggesting that zebra finches show consistent interindividual differences when foraging within flocks. Only the repeatability of arrival rank during the first session differed between the sexes and the magnitude of the finder's share was repeatable only in females during the first session. This lack of consistency suggests that individual zebra finches do not differ in their ability to secure a food patch they have just discovered, thus minimizing the role of interference competition, dominance and aggressiveness during scramble competition. This finding can be contrasted with a recent study by David et al. (2011) who reported that individual personality influences social dominance and preferential access to a single feeder in the same species. The discrepancy between the latter and the present study

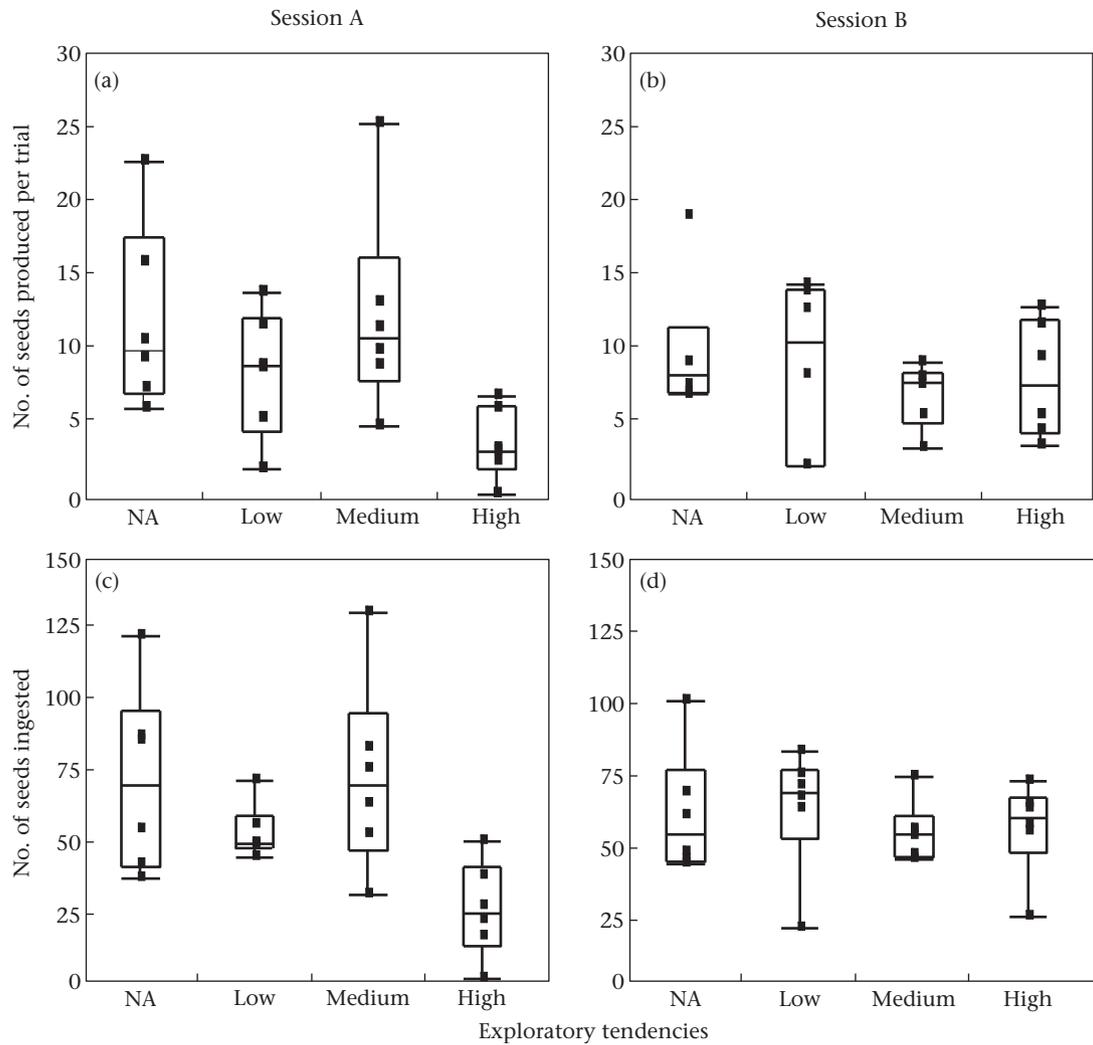


Figure 2. Influence of exploratory tendencies (NA, low, medium and high) on (a) the mean number of seeds produced per trial in session A, (b) the mean number of seeds produced per trial in session B, (c) the total number of seeds ingested in session A and (d) the total number of seeds ingested in session B. Boxes show the 75th and 25th percentiles and the median in between. Whiskers are computed as the 75th/25th percentile $\pm 1.5 \times$ the interquartile range. Black rectangles represent individual birds.

mainly lies in food availability, which was here greater (five seeds in 10 wells) than in David et al.'s (2011) study (a single feeder in a six-individual group; see Dubois & Giraldeau 2004 for a study on a related topic). This could explain why interference competition

seems to be minimal in the present study. Yet, even if aggressive interactions were nonexistent during trials, we cannot totally discard the possibility that dominant birds may intimidate their flockmates.

Table 3

Between-session variation in foraging behaviours recorded during producer–scrounger trials as a function of exploration categories

Measured variable	NA		Medium		High	
	%	<i>t, P</i>	%	<i>t, P</i>	%	<i>t, P</i>
Number of seeds produced	+5.0	16.71 <0.001	−27.7	14.64 <0.001	+118.2	6.81 0.002
Number of seeds scrounged	−51.0	−2.34 0.07	−38.0	−2.33 0.08	+18.0	−4.81 0.02
Proportion of seeds scrounged	−58.3	−2.24 0.08	−20.0	−2.8 0.05	−18.1	−5.17 0.01
Number of seeds ingested	−7.7	−11.45 <0.001	−28.8	−8.97 0.001	+47.2	−6.94 0.002
Finder's share	+12.0	−1.26 0.26	+3.5	−0.59 0.59	+58.2	−2.95 0.04

Statistical tests correspond to the significance of the difference between sessions A and B.

Although our experiments were performed on a small number of individuals, they were designed specifically to sort flockmates into different exploration tendency categories and so maximize within-flock variation in behaviour. Moreover, individuals were highly consistent in their behaviour within the same flock, reducing the likelihood of committing type I errors and confirming that observed variation was not the mere effect of random decisions. Although we only focused on exploratory behaviour, we are confident that our results can be generalized to global personality, as David et al. (2011) recently demonstrated that exploratory tendency was part of a wide behavioural syndrome including neophobia, risk-taking behaviour and activity in zebra finches.

We found that personality influenced the number of seeds that individuals ingested during scramble competition. Here high-exploratory individuals had a lower feeding success. Yet, this effect was found only during the first test session. High-exploratory birds adjusted their behaviour during the second session, and thus reached a similar success as individuals from the other exploration

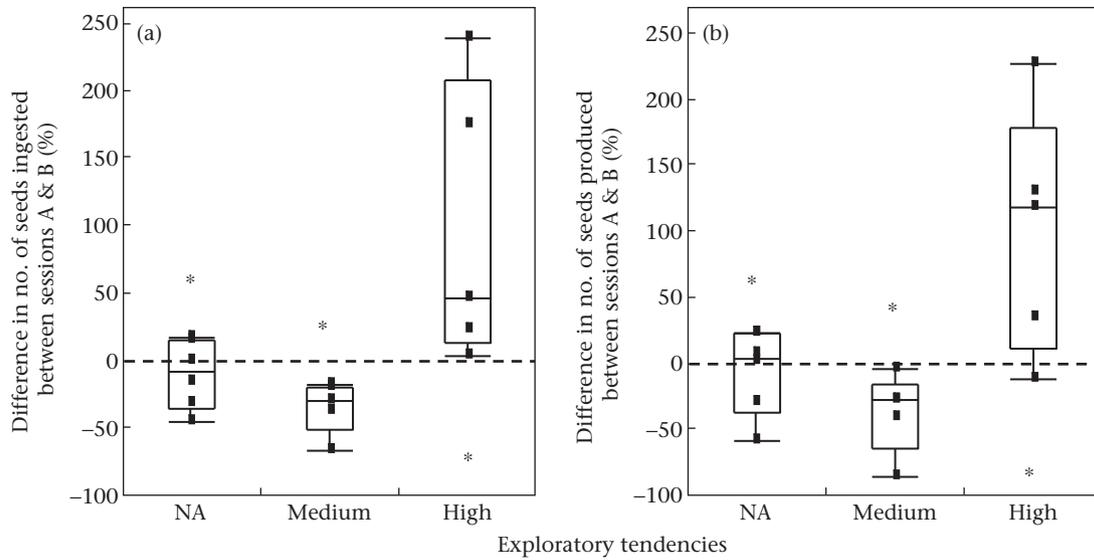


Figure 3. Influence of exploratory tendencies (NA, medium and high) on the difference in the individual number of seeds (a) ingested and (b) produced in the two different flocks between sessions. Asterisks indicate that the between-session change differs significantly from zero (shown by the dashed line). Boxes show the 75th and 25th percentiles and the median in between. Whiskers are computed as the 75th/25th percentile $\pm 1.5 \times$ the interquartile range. Black rectangles represent individual birds.

categories. A possible explanation for the observed change between sessions and the consequent lack of behavioural consistency could be that the influence of personality on individual behaviour is greater when individuals face a novel situation containing, in our case, both new conspecifics and unfamiliar foraging payoffs. When this happens, birds would rather be influenced by an intrinsic tendency, such as personality, because of a lack of experience, than try to learn

to adjust to the unfamiliar situation. Further experiments need to be designed to test the hypothesis that both personality and experience have interactive effects on foraging behaviour.

The lower patch production rate of high-exploratory individuals suggests that food-searching efficiency in zebra finches could be related to personality. For instance, [Beauchamp \(2006\)](#) showed in zebra finches that different individuals had different feeding

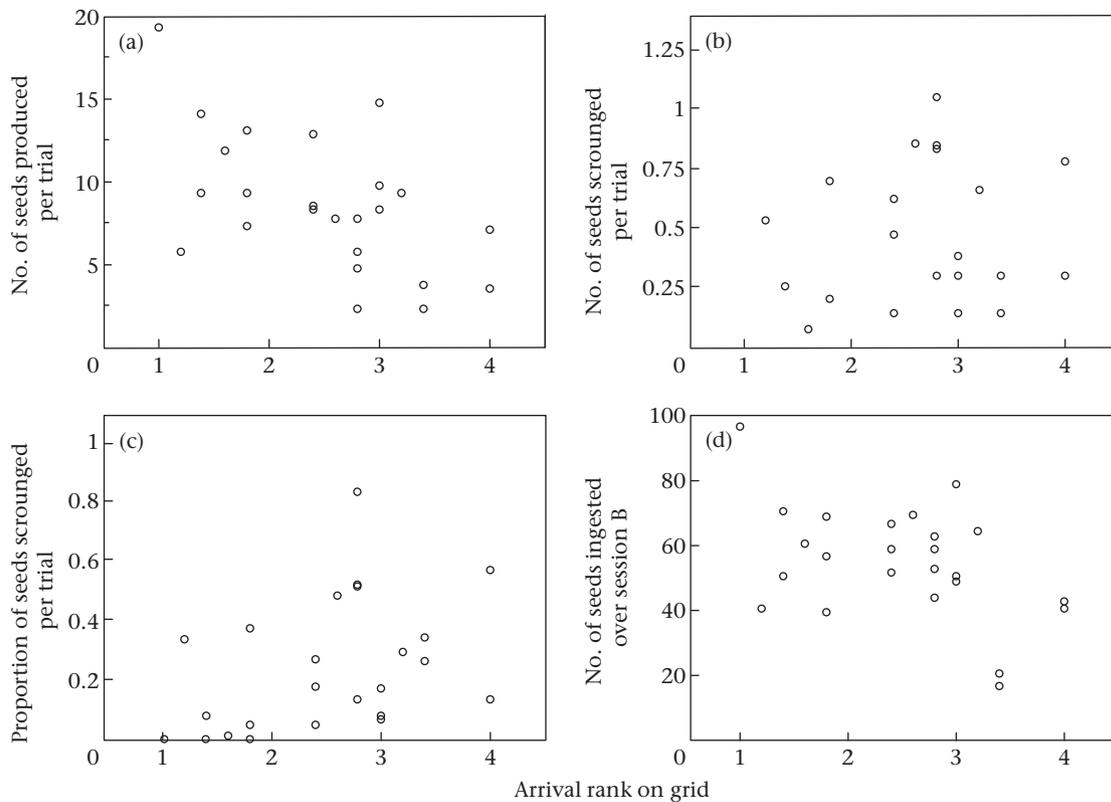


Figure 4. Correlation between arrival rank on the grid in session B and (a) the mean number of seeds produced per trial in session B, (b) the mean number of seeds scrounged per trial in session B, (c) the mean proportion of seeds scrounged per trial in session B and (d) the total number of seeds ingested over session B. Mean number of seeds scrounged per trial and mean proportion of seeds scrounged per trial were log transformed to reach normality.

efficiencies, measured as the number of seeds an individual can find on a grid in a given time period. Moreover, less efficient birds scrounged more in subsequent producer–scrounger games. Future studies should explore the possibility that variation in personality could be related to a so-called ‘speed–accuracy trade-off’ (Chittka et al. 2009), linked to foraging efficiency. In foraging zebra finches, we would expect high-exploratory individuals to be faster at sampling the grid while being less accurate in detecting seeds. In contrast, less exploratory birds should be slower at sampling wells but less likely to miss the full ones.

We did not find any effect of personality on the propensity to use social information when foraging (i.e. scrounging). This result can be contrasted with those of two related studies: a study of the barnacle goose (Kurvers et al. 2010) and another on zebra finches (Beauchamp 2006). Our results differ from those obtained with the barnacle goose in which ‘reactive’ individuals (less exploratory individuals in the present study) scrounged more than ‘proactive’ ones (Kurvers et al. 2010). This difference may be associated with the link between personality and landing order between the two species. Indeed, in foraging barnacle geese, proactive individuals are more likely to be found leading the group, while reactive individuals are more likely to follow (Kurvers et al. 2009). Proactive individuals are more likely, therefore, to be the first to arrive on food patches while reactive ones join others’ discoveries and scrounge. In zebra finches, the link between scrounger tactic use and arrival rank on food patch was documented by Beauchamp (2006) and the present study, but unlike for the barnacle goose, we found no link between exploratory tendency and arrival rank on the grid (but see Beauchamp 2000).

A recent study conducted on zebra finches found that high-exploratory individuals were dominant and had preferential access to a single feeder in interference competition (David et al. 2011). These results are in contrast to those we obtained here. Taken together, they suggest that individuals of the same personality type may be variably successful in different competitive contexts, and thus face different selection pressures in different competitive situations. High-exploratory individuals may be more successful in interference competition but less successful in scramble competition. These differential effects of competition could play a role in the maintenance of personality variation within populations. Following this reasoning, the extent to which individuals of a given species are subject to each type of competition during their lives can influence the type of personality that will be ultimately selected in competitive contexts.

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