Individual determinants of social foraging tactic use when resources are defendable: an experiment with zebra finches

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Abstract

In a social foraging context where individuals can search either for food (i.e. produce) or for opportunities to join (i.e. scrounge), bold individuals, generally, tend to produce more than shy individuals. Yet, the underlying cause of this link remains poorly understood. In particular, bold individuals might rely more on the producer tactic because they have less chance to detect joining opportunities compared to shy individuals or because they prefer more risky and uncertain behavioural tactics. To assess the importance of both mechanisms, we conducted a laboratory experiment with zebra finches (*Taenyopigia guttata*) that were observed while searching for defendable food patches using either the producer or the scrounger tactic, when their arrival order on the grid was either free or imposed by the experimenter. As anticipated, we detected a strong effect of neophobia on producer-scrounger tactic use, but contrary to most previous experiments in which food patches were not defendable, shy individuals, in the present study, relied more on the producer tactic. In addition, we found that arrival order had no significant effect on foraging tactic use in bold and shy individuals. Thus, our results support the hypothesis that producer-scrounger tactic use would not be determined by the ability of individuals to detect scrounging opportunities, but rather by their tolerance to uncertainty and risk. Furthermore, our findings have important evolutionary implications as they suggest that temporal and/or spatial heterogeneity in resource distribution, through influencing the success of each behavioural type, would contribute in maintaining personality differences within populations.

Keywords: Personality differences, Neophobia, Risk-taking tendency, Arrival order, Producer scrounger game, Contest competition.

Introduction

Several studies have demonstrated that personality differences among individuals may influence their behaviour in various contexts, but the underlying cause of this link generally remains poorly understood. For instance, in a social foraging context where animals can either search for their own food (i.e. produce) or exploit the resources discovered by others (i.e. scrounge), individuals typically differ in their foraging tactic use depending on their personality, with both direct and indirect evidence indicating that bold individuals tend to rely more on the producer tactic than shy individuals (Kurvers et al. 2010; Carter et al. 2013; Aplin et al. 2014; Aplin & Morand-Ferron 2017). Yet, this pattern might be explained by at least two different mechanisms. First, bold individuals would be more likely to adopt the producer tactic, simply because they have less chance to detect joining opportunities. This could be the case because either they enter a foraging area first which constrains them to rely more on the producer tactic (Dubois et al. 2012) or they have a higher tendency to stay far from others (Ward et al. 2004; Cote et al. 2008; Jolles et al. 2015). According to this hypothesis, the stronger tendency for shy individuals to scrounge would then be a by-product of their reactive personality. Second, individual differences in foraging tactic use would reflect differences in risk-taking tendency. More precisely, bold individuals are expected to preferentially use behavioural alternatives that are more risky and whose consequences, therefore, are more uncertain, whereas shy individuals, on the contrary, are expected to rely more on behavioural tactics that are less risky and uncertain (Coleman & Wilson 1998). Given that an individual, in general, has a higher risk of obtaining no food as a producer than as a scrounger, bold individuals should then rely more on the producer tactic than shy individuals.

Although some previous studies have found support for the hypothesis that individual differences in the propensity to lead are associated with differences in social information use (Faria et al. 2010; David et al. 2014), the observed correlation might be explained by other personality or physiological traits that are usually associated with leadership, such as boldness (Beauchamp 2000; Harcourt et al. 2009; Kurvers et al. 2009; Schuett and Dall 2009), activity (Beauchamp 2000) or energetic requirements (Bousquet et al. 2017). To distinguish between these two hypotheses (i.e. differences among individuals in either the opportunities to scrounge or their risk-taking tendency), therefore, one needs to manipulate the factors thought to influence the capacity of individuals to detect scrounging opportunities or the level of risk associated with both foraging tactics. Specifically, if differences among individuals in their foraging tactic use reflect differences in their chance of detecting scrounging opportunities, they should adjust their behaviour according to their arrival order. More precisely, we would then expect shy individuals to increase their use of the producer tactic when they are forced to enter a foraging area first, while bold individuals should rely more on the scrounger tactic when they are among the last to arrive. Alternatively, if the often-observed negative correlation between boldness and scrounger tactic use arises because personality types differ in their risk-taking tendency, the effect of boldness on producer-scrounger tactic use might vary depending on ecological conditions. Notably, the relationship between boldness and foraging tactic use has been mainly investigated, to date, in a scramble competition context, in which producing is a more risky and uncertain tactic than scrounging (Wu & Giraldeau 2005). When resources are defendable, however, producing should be less risky and uncertain than scrounging. Indeed, given that a food discoverer obtains a finder's advantage before the joiners arrive, the possibility that a producer receives a zero payoff is then lower than the possibility of a scrounger receiving a zero payoff (Barta & Giraldeau 1998; Giraldeau & Caraco 2000). The risk of getting nothing would be particularly high for shy individuals as they are generally less aggressive than bold individuals (Sih et al. 2004) and hence would rarely succeed in defending a food patch against conspecifics. In the context of contest competition, therefore, we would expect a positive correlation between boldness and scrounger tactic use if foraging tactic is determined by the ability of individuals to cope with uncertainty.

To assess the relative importance of arrival order and risk-tendency on individual foraging tactic use, and better understand the link between personality and social information use, we then conducted a laboratory experiment with zebra finches (*Taenyopigia guttata*) that were observed while searching for defendable food patches using either the producer or the scrounger tactic. We used flocks of zebra finches since two previous studies have demonstrated that producer-scrounger tactic use is affected by arrival order when food patches can be shared (Beauchamp 2006; David et al. 2014), with first arriving individuals producing more compared with later arriving individuals. However, those previous studies could not rule out other explanations as none of them had manipulated the arrival order of the birds. In the present study, all foraging groups which were composed of bold, shy and intermediate individuals in equal proportion, were then tested first in a treatment where the arrival order of the subjects on the grid was free and second in a treatment where arrival order was imposed by the experimenter, who then forced the focal individual to land first or last.

Material and methods

(a) Subjects and housing conditions

We used 18 female zebra finches of approximately three years of age. All the birds came from a local breeder (Exotic Wings & Pet Things, St Clements, Ontario, Canada) and were marked with coloured leg bands for identification. Outside experimental sessions, they were housed in same-sex cages (38×38×48 cm) with a maximum of three individuals per cage under a 12: 12 h dark: light photoperiod at a temperature of 23 ± 1 °C, and had unlimited access to fresh water, seeds, cuttlefish bone, oyster shell and egg food supplement. The experiments described in this study were approved by the Animal Care Committee of the University of Montreal (animal care permit #15-040) and conformed to all guidelines of the Canadian Council on Animal Care.

(b) Personality assays

Before we observed the birds' foraging tactic use, we estimated their neophobia using the novel object test procedure. The birds were tested individually in their home cage and were subjected to four trials (i.e. two control trials and two trials with a novel object) with a one-week delay between two consecutive trials and after one night (12 h) of food deprivation. One hour before each trial, the focal bird was isolated in its home cage with only a water dispenser and two perches. We then placed a feeder filled with seeds into the cage as well as, except for the control trials (i.e. the first and third ones), a novel object close to the feeder, and we measured the latency before the focal bird started feeding. For the second and fourth trials, we used two different objects of the same size, and balanced the order of presentation. A trial was over when the bird started eating or after 10 minutes, whichever occurred first. After the birds had completed the four trials, we calculated their neophobia score as the average latency time to start eating with a novel object minus the average latency time to start eating without a novel object. For all the birds tested, the mean (± SEM) neophobia score was equal to 334.27 sec ± 49.58. The birds were then classified into three categories (i.e. shy, intermediate and bold) that each contained six subjects.

(c) Producer-scrounger experiment

We conducted the experiments in an indoor aviary (155 × 225 × 240 cm). The birds were observed through a one-way mirror while searching for food on a 120 ×120 cm wooden table on which 49 circular holes (1.91 cm diameter, 1.27 cm deep and that were placed 15 cm apart from each other) served as food patches. Each patch was surrounded by three cardboard partitions arranged to prevent competitors from feeding simultaneously from the same food patch, thus promoting resource defense. Three flocks, each composed of six individuals, were tested under two different treatments where the arrival order of the subjects on the grid was either free or imposed by the experimenter, who then forced the focal individual to land first or last. Each flock was composed of two shy, two bold and two intermediate individuals and the composition of the groups remained identical among the two treatments, except for one group in which we had to remove and replace two individuals after the first treatment, because of injuries. Under the two treatments, the birds were introduced before the beginning of a trial into individual boxes (15 × 15 × 15 cm) that were placed next to each other in front of the grid and that could be opened by the experimenter from outside the aviary. In the first treatment, where the arrival order of the birds was free, the experimenter opened all boxes simultaneously, while in the other treatment where the arrival order was constrained, each box was opened 10 s after the previously released bird had landed on the grid.

For each trial, only five randomly chosen patches contained five millet seeds. Each flock experienced six consecutive trials per day with a 15 minutes inter-trial interval. After they had been familiarized with the environment, the birds were submitted to the two treatments in the same order after a 12 hour-period of food deprivation for a total of 15 testing days: they experienced five consecutive days of testing during which their arrival order was free, then five other consecutive days of testing during which they were forced to land first and finally five other consecutive days of testing during which they were forced to land last. For each 5-day period, the first two days were used as training sessions while the remaining three days were used for data collection. Each trial started when the first bird landed on the grid and ended 10 minutes later or when the focal bird had left the grid for more than one minute. For each focal bird, we recorded its order of landing as well as the number of successful finding and joining events. In a finding event, an individual discovered and fed from a food patch at which no other individual was present. By contrast, in a joining event, the focal bird ate at least one seed from a food patch where another individual was already foraging. After a series of six trials was completed, the birds were returned into their respective home cages.

(d) Statistical analyses

For each individual, we calculated the proportion of finding events every testing day as the number of finding events divided by the sum of the number of finding and joining events. To test whether the birds were consistent in their foraging tactic use and arrival order, we estimated the repeatability of both traits from the intra-class correlation coefficient (ICC) and calculated the confidence intervals following Nakagawa and Schielzeth (2010). We also investigated whether individual differences in arrival order were explained by differences in neophobia using a linear mixed-effects model where the arrival order and neophobia were entered as the dependent and the independent variables, respectively. For these analyses, we only considered data from the first treatment where the arrival order of the birds was not constrained.

Finally, to determine whether the strategy used by the birds was influenced by their neophobia or arrival order, we ran a linear mixed-effects model; the frequency of producing events was entered as the dependent variable while the neophobia, arrival order and treatment were considered as fixed factors, and the day of testing and the flock were included as random factors.

Statistical analyses were performed with SPSS 23.0.

Results

While the birds were consistent in their foraging tactic use across trials (R=0.382; 95% CI: 0.047 to 0.717), their arrival order on the grid was not significantly repeatable (R= 0.219, 95% CI = -0.131 to 0.569). Yet, arrival order was marginally associated with neophobia ($F_{1, 17}$=1.177, *P*=0.079), indicating that individuals with longer latency times tended to land later on the foraging grid (Fig. 1).

Individual differences in the frequency of finding events were mainly attributable to differences in neophobia (Table 1), with shy individuals having a higher proportion of finding events compared to intermediate and bold individuals (Fig. 2). In addition, the effect of arrival order depended on the neophobia of the birds, as revealed by a significant interaction between the two factors (Table 1). Accordingly, we found that arrival order had no effect on the proportion of finding events in shy ($F_{1,5}$=0.565, *P*=0.726) and bold ($F_{1,5}$=1.314, *P*=0.281) individuals, while birds among the first to land had a higher proportion of finding events in intermediate individuals ($F_{1,5}$=2.481, *P*=0.048; Fig. 3A). By contrast, shy individuals had a higher proportion of finding events in the second treatment in which their arrival order was constrained than in the first treatment ($F_{1,5}$=4.535, *P*=0.040; Fig. 3B), while the treatment had no effect on foraging tactic use in bold ($F_{1,5}$=1.692, *P*=0.201) and intermediate ($F_{1,5}$=1.000, *P*=0.324) individuals.

Discussion

As anticipated, we found that the birds were consistent in their use of foraging tactic and that producer-scrounger tactic use was strongly affected by neophobia. Yet, contrary to most previous studies (Kurvers et al. 2010; Carter et al. 2013; Aplin et al. 2014; but see Jolles et al. 2013), shy individuals relied more on the producer tactic than bold and intermediate individuals. Furthermore, although shy individuals tended to land later on the foraging grid compared to bold and intermediate individuals, arrival order was not significantly repeatable and we found that the timing of landing influenced individual tactic use decision only in individuals with intermediate latency times. By contrast, arrival order had no effect on foraging tactic use in bold and shy individuals. This finding apparently contradicts two previous studies (Beauchamp 2006; David et al. 2014) that detected a positive association between arrival order and producer tactic use in zebra finches. In both studies, however, the order in which the birds landed on the foraging grid was not constrained by the experimenter, and the reported effect, therefore, could have been due to other factors that are associated with leadership. In support to this hypothesis, David et al. (2014) found that the effect of arrival order on producer-scrounger tactic use, persisted even once all the birds had landed on the foraging grid, and hence had *a priori* all the same chance of finding opportunities to join others' food discoveries. Taken together, previous studies and our findings, therefore, strongly suggest that individuals that mainly use the producer tactic in a scramble competition context would not behave as they do because they lack opportunities to scrounge, but because they prefer more risky and uncertain behavioural tactics. This conclusion is further supported by the fact that shy individuals in the present study relied more on the producer tactic when their arrival order was determined by the experimenter rather than uncontrolled, as this result confirms that shy individuals would be particularly sensitive to social cues and hence would only rely on the scrounger tactic under very limited conditions when this tactic is particularly risky and uncertain.

Our findings have important evolutionary implications as they suggest that temporal and/or spatial heterogeneity in resource distribution would contribute in maintaining personality differences within populations. Specifically, previous studies and our results have demonstrated that depending on resource distribution or accessibility, and hence on the level of resource defendability, individuals relying more on the scrounging tactic may be either the shyest individuals when the resources are not defendable, or the boldest individuals when food patches can be monopolized. Yet, several studies have found that individuals generally have a strong preference for the foraging tactic that provides them with the highest possible fitness return (Beauchamp 2006; Katsnelson et al. 2011). For example, zebra finches who are less efficient at obtaining food (i.e. playing producer) preferentially use the scrounger tactic (Beauchamp 2006), while house sparrows (*Passer domesticus*) with better learning abilities rely mainly on the producer tactic (Katsnelson et al. 2011). A number of studies have demonstrated that differences among individuals in their foraging ability may be associated with personality traits such as exploration (Guillette et al. 2009; David et al. 2011) or neophobia (Boogert et al. 2006). If the skills required to forage efficiently vary depending on ecological conditions, however, one could expect that the performance of each personality type will change over time, thereby contributing in the maintenance of individual differences within populations. Consistent with this idea, Montiglio et al. (2017) reported that stream water strider males (*Aquarius remigis*) exhibiting higher activity and aggressiveness had a higher mating success than less active and aggressive males, but only when the level of mating competition among males was low, while this advantage progressively disappeared as the number of competing males increased. In zebra finches, David et al. (2011) also found evidence that low-exploratory birds were more efficient in finding food and had a greater feeding success compared to high-exploratory individuals in scramble competition, probably because they were more accurate in detecting seeds. Since low-exploratory individuals are generally subordinate, however, this advantage might disappear when resources are defendable. Thus, additional experimental and theoretical studies would be required to examine how personality differences influence individual tactic use and foraging success under different ecological conditions that prevent or promote resource defense.

In conclusion, the present study strongly suggests that foraging tactic use decision would not be determined by the ability of individuals to detect scrounging opportunities, but rather by their tolerance to uncertainty and risk. Although we detected no significant effect of arrival order on tactic use, individuals with short and intermediate latency times had nevertheless a higher proportion of finding events when they landed first on the foraging grid than when they were introduced last. By contrast, individual tactic use was affected by the experimental treatment in shy individuals that are more sensitive to social cues. Thus our results indicate that individuals with different behavioural types would be sensitive to different cues. Finally, given that we found an opposite effect of neophobia on producer-scrounger tactic use compared to most previous studies, our findings support the idea that temporal and/or spatial heterogeneity in resource distribution, through influencing the success of each behavioural type, would contribute in maintaining personality differences within populations.

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Figure legend

Figure 1. Differences among bold, intermediate and shy individuals in their: A) mean (±SEM) arrival order and B) mean (±SEM) proportion of finding events.

Figure 2. Mean (±SEM) proportion of finding events in bold, intermediate and shy individuals depending on whether: A) the bird was the first (black bars) or the last (grey bars) to land on the grid, and B) the arrival order of the subjects on the grid was free (black bars) or imposed by the experimenter (grey bars).

Table 1. Results from the linear mixed-effects model examining the effects of neophobia, landing order, treatment and their interactions on the proportion of finding events.

Variable	df	*F*	*P*
Neophobia	**17**	**7.289**	**0.001**
Landing ordrer	5	0.225	0.950
Treatment	1	1.058	0.311
Neophobia x Landing order	**29**	**1.998**	**0.010**
Neophobia x Treatment	5	1.511	0.204
Landing order x Treatment	1	0.014	0.906

363 **Figure 1**

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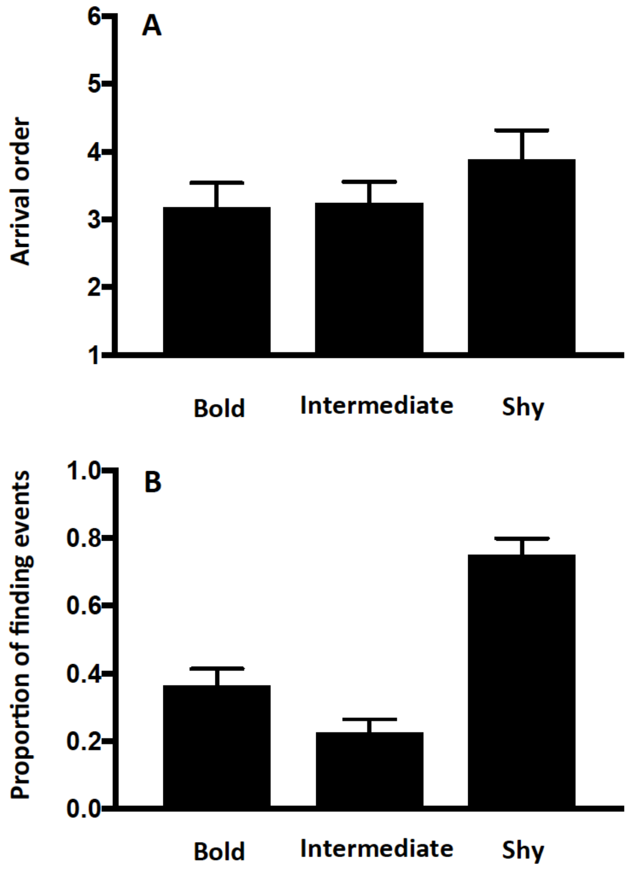
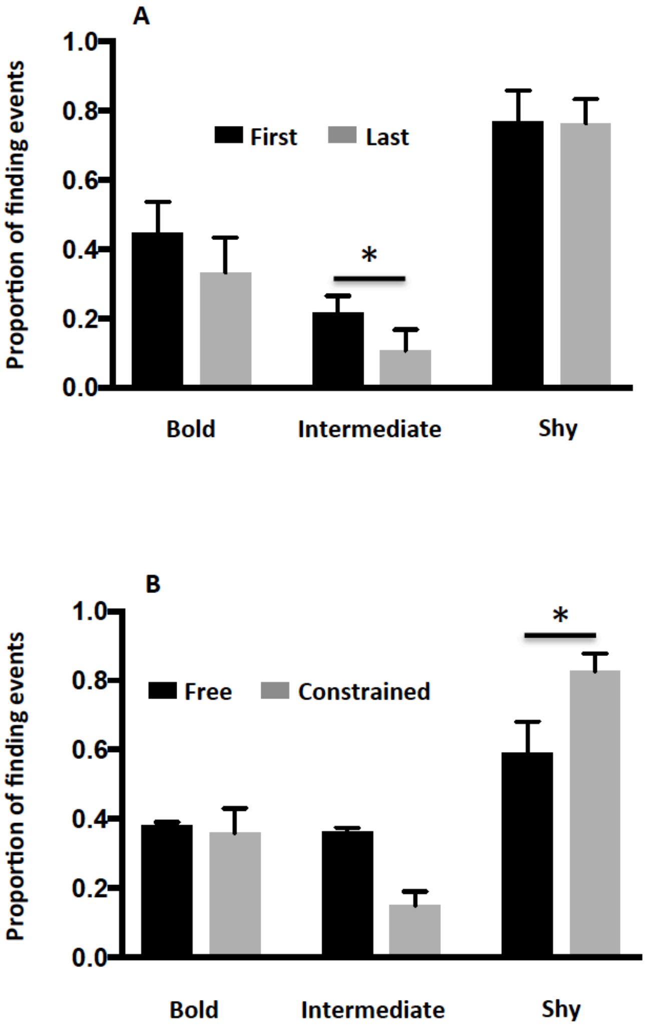


365

Figure 2


A
Proportion of finding events
1.0
0.8
0.6
0.4
0.2
0.0
First
Last
*
Bold
Intermediate
Shy
B
Proportion of finding events
1.0
0.8
0.6
0.4
0.2
0.0
Free
Constrained
*
Bold
Intermediate
Shy