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Persistent individual differences in tactic use in a producer–scrounger game are group dependent

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Consistent individual differences in behaviour have now been documented in a broad range of organisms over a variety of contexts. However, individual differences in social contexts have received less attention. We explored the consistency and temporal persistence of individual differences in tactic use in a producer–scrounger foraging game using two sets of flocks of wild-caught nutmeg mannikins, *Lonchura punctulata*. With both sets of birds, we observed significant individual differences in tactic use that persisted under different food distributions and when flock members were reunited at a 6-month interval with the same flockmates but not when flock members were different. In another experiment, in which birds with high-scrounging profiles were made to forage in the same flock, the corporate frequency of scrounging was no higher, and the intake rate no lower than in flocks made up of intermediate- or low-frequency scroungers. Taken together our experiments suggest that persistent individual differences can arise from dynamics that are peculiar to the group in which they occur, underlining the importance of companions' identity in determining tactic use in this game. Behavioural plasticity can erase idiosyncratic individual differences in games with frequency-dependent payoffs when group composition changes.

Frequency-dependent selection has long been suggested to maintain phenotypic variation within populations (reviewed in Ayala & Campbell 1974; Sinervo & Calsbeek 2006). More recently, it has also been suggested as a potential mechanism for the maintenance of consistent individual behavioural differences or personality (Dall et al. 2004; Wolf et al. 2008; Dubois et al. 2010). Evolutionary games are characterized by frequency-dependent payoffs (Giraldeau & Caraco 2000) and are often couched in arguments of frequency-dependent selection acting on alternative strategies. However, in many cases where behavioural tactics are studied, tactic use results from a decision based on apparent estimation of the frequency-dependent payoffs provided by each available alternative (Giraldeau & Dubois 2008). When this is the case, focusing only on average group effects (Bergstrom & Godfrey-Smith 1998; Wischniewski et al. 2009) may prevent researchers from observing idiosyncratic differences in tactic selection between players. On the other hand, studies focusing on individual differences and personality have mostly examined nonsocial behaviour (Magnhagen & Bunnefeld 2009; Réale & Dingemanse 2010), and so have not appreciated the effect of frequency dependence that characterizes social behaviour. A growing number of studies report individual differences in tactic use emerging within game-theoretical contexts such as the dictator, public goods (e.g. Kurzban & Houser 2001; Knafo et al. 2008) and producer–scrounger (PS; e.g. Beauchamp 2001; Mathot et al. 2009) games. We explored the role of frequency-dependent tactic adjustment in the emergence of such individual differences in a social and hence game-theoretical context using a PS game.

In a PS game, producer is the tactic that searches for a resource, while scrounger exploits this investment (Barnard & Sibly 1981). Examples of PS games include alternative mating tactics, brood parasitism, kleptoparasitic interactions for food as well as social information use (Barnard 1984; Giraldeau & Dubois 2008). Studies on foraging PS systems have shown that members of a group can adjust their tactic use under conditions calling for different equilibrium frequencies of scrounger (Mottley & Giraldeau 2000) but still exhibit consistent individual differences (Morand-Ferron et al. 2007). These individual differences might result from intrinsic phenotypic differences that affect the costs and benefits of playing scrounger and so constrain individuals to using mostly one or the other tactic. The most common example of such an intrinsic

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phenotype-limited game concerns the effect of social dominance on PS tactic use (Barta & Giraldeau 1998). In cases where social hierarchy tends towards despotism, only dominant individuals can use the scrounger tactic (Barta & Giraldeau 1998; Liker & Barta 2002; McCormack et al. 2007; King et al. 2009). Another source of individual differences does not invoke intrinsic phenotypic differences but rather the frequency dependence of rewards that can constrain individual learning within groups (Giraldeau 1984; Giraldeau & Caraco 2000). For a similar investment in each tactic, some group members will inevitably find food first (because of ubiquitous heterogeneity of food distribution in natural environments) and will therefore be rewarded for producing again. While producing increases, it creates increasing opportunities for others to scrounge the discoveries and so to be rewarded for scrounging (Giraldeau 1984; Giraldeau & Dubois 2008). So, when an individual's allocation to each tactic is governed by the rewards it experienced in the past (Katsnelson et al. 2008; Morand-Ferron & Giraldeau 2010), individuals that first discovered food should exhibit a higher tendency to search for food. Similarly, those that were rewarded for joining initially should tend to look for further scrounging opportunities. The frequency-dependent reward dynamics in this situation can create persistent individual differences between otherwise phenotypically equal players, or can contribute to reinforcing consistent individual differences fostered by phenotypic differences.

While some intrinsic phenotypic constraints to the use of scrounger such as age (Bugnyar & Kotrschal 2002), sex (Pfeffer et al. 2002), basal metabolic rate (Mathot et al. 2009), foraging efficiency (Beauchamp 2006) and exploratory tendencies (Marchetti & Drent 2000; Kurvers et al. 2009), have been documented on short timescales, the long-term persistence of individual differences in scrounger use have not yet been assessed. Moreover, the consistency of these individual differences across different group compositions has received very little attention (but see Beauchamp 2001), even though empirical evidence is accumulating for companion-dependent effects on individual characteristics, such as the expression of a learned foraging technique (Drea & Wallen 1999), exploration (Schuett & Dall 2009) and risk-taking behaviour (Piyapong et al. 2010).

In this study, we first examined the persistence of individual differences in scrounger use in wild-caught nutmeg mannikins, *Lonchura punctulata*, tested at a 6-month interval with the same flockmates, and then explored the effect of foraging with a new set of companions (Experiment 1) or companions assorted according to their previous level of using the scrounger tactic (Experiment 2). If scrounger use was constrained genetically or by an intrinsic stable phenotypic trait, we expected individual differences to persist over time and different flock compositions. Moreover, we expected assorted high-scrounging individuals to scrounge persistently more than other individuals, and consequently obtain lower payoffs than assorted low- or intermediate-scrounging birds. In contrast, if individual differences in scrounger use were due to companion-dependent phenotypic traits or to frequency-dependent learning effects, we expected individual differences to persist as long as flock composition was stable, but to change as soon as groups were assorted differently, and all assorted groups to obtain equal payoffs.

METHODS

Subjects

We used flocks of wild-caught nutmeg mannikins, small seed-eating finches that feed socially without much aggression (Goodwin 1982; Immelman 1982). Captive flocks of mannikins have been shown to conform to the main assumptions of the PS game such as tactic incompatibility (Coolen et al. 2001) and negative frequency dependence of payoffs (Mottley & Giraldeau 2000).

Wild-caught nutmeg mannikins were purchased from a commercial supplier (L'oisellerie de l'Estrie, Québec, Canada) and individually identified with a unique combination of coloured leg bands. They were kept on a 12:12 h light:dark cycle at temperatures of 21–23 °C. To reduce the number of individuals used in experiments, we selected birds from the existing colony and returned all individuals to the colony after trials were completed. Birds had ad libitum access to perches and water at all time, and to ground oyster shells and a seed mixture (canary seed and vitamin-supplemented white, red, golden and Siberian millet seed) outside experimental trials. Newly formed flocks were always allowed a minimum of 3 days with ad libitum feeding in regular containers before beginning experimental trials. Experiments were conducted under Animal Use protocols 465, 600 and 601 of Université du Québec à Montréal.

Experiment 1

We conducted all experiments in aviaries (area: 2.4 m^2; height: 2.4 m) under identical light and temperature conditions. We randomly arranged 12 birds into three flocks of four individuals ('initial' flocks). We allowed each flock to familiarize itself to the aviary for 4–5 days prior to testing. The flocks searched for seed clumps on a wooden table (1.0 × 0.7 m) onto which a grid of 99 patches (1.3 cm diameter; 1.0 cm deep) had been drilled at 10 cm intervals between centre points to serve as food patches. We tested the birds on 6 consecutive days. We food-deprived each flock for 15 h (overnight plus 3 h after lights on) before each test day and conducted four tests per day at 30 min intervals. For each test, the experimenter put five seeds in each of 10 randomly selected patches (10 × 5 seeds). We videotaped a different bird during each test (order balanced through days). Using the Noldus Video-Pro 4.0 software (Noldus Information Technology, Wageningen, The Netherlands), we noted the number of patches it produced (discovery of a new patch) and scrounged from (i.e. feeds from a patch discovered by a producer). After the 6 days of testing, the birds were returned to their original cages in the colony.

Six months after tests on the initial flocks were completed, we reassembled the same flocks and tested them again over 4 consecutive days ('reassembled' flocks). We used the same procedure as for initial flocks, but randomly selected five patches, each of which received 10 seeds (5 × 10 seeds). Immediately after testing the last reassembled flock, we randomly reassorted the 12 birds into three new flocks. The 'shuffled' flocks were composed of two individuals from the same initial flock and the remaining two from two different initial flocks. We tested shuffled flocks following the same procedure as for the reassembled flocks over 5 consecutive days.

Experiment 2

We used four flocks of five birds from our colony, none of which had participated in the first experiment. We allowed the first two flocks ('initial flocks') to forage in an aviary (1.5 × 3.8 m and 2.3 m high) on a 99-patch grid over 21 days. One flock ('a'; see Appendix Table A1) encountered the following sequence of food distributions: 20 patches of 10 seeds (20 × 10 seeds) for 8 days, 100 patches of two seeds (100 × 2 seeds) for 8 days, and 20 × 10 seeds again for 5 days. Conditions for the other flock ('b' in Table A1) were the same except during the first 8 days, when 40 patches were baited with five seeds each (40 × 5 seeds). We ran 10 trials per day at hourly intervals, and collected data on one focal bird per trial, with time of day counterbalanced for the birds over days. All birds were then returned to randomly chosen cages of the colony for 6 months.

After this period, we ‘reassembled’ the same two flocks and allowed them to forage for another 21 days in the same conditions, but exchanged the sequence of food distribution. We also formed a third and fourth flock (‘for assortment’ under ‘c’ and ‘d’ in Table A1) and allowed them to forage in similar conditions (food distribution alternated between 100 × 2 seeds and 20 × 10 seeds every 2 days during the first 16 days). In the last 5 days of this experiment, all four flocks were foraging on the 20 × 10 seeds distribution. We ranked each bird within its own flock in terms of mean proportion of patches scrounged in this food distribution, and 2 days later, formed four ‘assorted’ flocks: one was composed of the top producer from each flock plus the bird with the lowest mean proportion of patches scrounged among all remaining birds (producer flock), another was composed of the top scrounger from each flock plus the bird with the highest proportion of patches scrounged among remaining birds (scrounger flock), while the remaining birds were haphazardly distributed among two flocks (intermediate flocks). We submitted these four ‘assorted’ flocks to the same conditions: 20 × 10 seeds, 5 × 40 seeds, and finally 100 × 2 seeds distributions. Each condition lasted 3 days, with five trials per day per flock. We then returned the birds to randomly chosen cages of the colony.

Finally, we used two new birds and eight birds from the third and fourth flocks to form two flocks (‘c’ and ‘d’ in Table A1) that were tested in their ‘initial’ and ‘reassembled’ flocks as described above. Data from initial and reassembled groups are from trials run in the context of another experiment (Morand-Ferron & Giraldeau 2010), which explains why some details of the procedure differ from those of experiment 1, and sometimes varied among flocks. Overall, all birds used for initial and reassembled flocks experienced the same conditions, but in a different order (see Table A1). For each trial, we recorded the number of patches produced and scrounged by the focal bird. To include only trials in which birds showed sufficient motivation to feed, we excluded from analysis all trials for which the focal bird ate from two patches or less ($N = 79$ out of 1860 trials). Individuals were then characterized by their mean proportion of patches scrounged over all trials for initial, reassembled or assorted flocks.

Statistical analyses

We investigated the presence of individual differences in tactic use in initial flocks by comparing the likelihood of a generalized linear mixed model (GLMM) with a binomial error distribution, including a random term for individual and flock with that of a model excluding the intercept for individual (Pinheiro & Bates 2000) using R version 2.9.1 and 2.10.0 (R Development Core Team 2009). The response variable was a two-column matrix composed of the number of patches scrounged and produced by the focal bird, thereby representing the proportion of patches scrounged at each trial (package ‘lme4’, family = binomial; Crawley 2007). The models controlled for food distribution and day, whenever appropriate. We assessed the persistence of individual differences in tactic use (arcsine-transformed proportion of patches scrounged) between treatments using correlation tests. A partial correlation analysis controlling for flock (Kendall correlation tests on ranks for proportion of patches scrounged within a flock) gave similar results for persistence of scrounger use over a 6-month period in experiments 1 and 2 (not shown). To test for differences in scrounger use in assorted flocks from experiment 2, we again used GLMM with a binomial error distribution. We specified individual as a random effect, but this time we examined the significance of the fixed effect ‘assorted flock type’ (scrounger versus producer and intermediate flocks) separately for each food distribution. When examining differences in intake rate among flock types, we used a linear mixed model on the log-transformed intake rate (number of seeds obtained using both tactics divided by time spent on the foraging grid during each trial), with individual as a random effect. We repeated this analysis separately for each food distribution.

RESULTS

Experiment 1

Significant individual differences in tactic use were present in the first three flocks tested ($\chi^2_1 = 48.4$, $P < 0.001$). These differences persisted after the 6-month period as evidenced by the positive correlation between tactic use in initial and reassembled flocks ($r_{10} = 0.68$, $P = 0.015$; Fig. 1a). Tactic use in the shuffled flocks, on the other hand, was not significantly correlated with tactic use in reassembled flocks ($r_{10} = -0.12$, $P = 0.70$; Fig. 1b) or in initial flocks ($r_{10} = 0.11$, $P = 0.73$; Fig. 1c).

Experiment 2

Experiment 2 revealed similar results with different birds: there were significant individual differences in tactic use between the birds (initial flocks: $\chi^2_1 = 666.6$, $N = 20$, $P < 0.001$). These individual differences were consistent across different food distributions (40×5 versus 100×2 in initial or reassembled flocks: $r_{18} = 0.89$, $P < 0.001$; 100×2 versus 20×10: $r_{18} = 0.83$, $P < 0.001$),

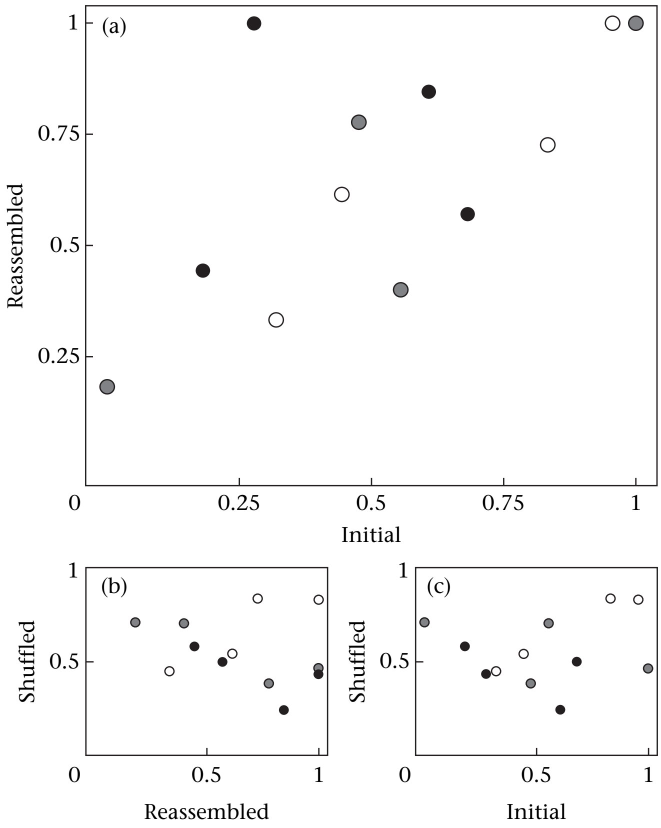

Figure 1. Individual scrounger use (mean proportion of patches scrounged) for 12 nutmeg mannikins, from (a) initial to reassembled flocks, (b) reassembled to shuffled flocks, and (c) initial to shuffled flocks. Birds from the three different initial flocks are shown in white, grey and black.

and persisted when birds were tested with the same companions at a 6-month interval (initial versus reassembled: $r_{18} = 0.68$, $P = 0.003$; Fig. 2a). However, the correlation did not hold when flock composition was changed (before versus after assortment: $r_{18} = 0.41$, $P = 0.07$; Fig. 2b). We found a significant correlation in individual scrounger use when restricting analysis to the food distribution just preceding and just following assortment ($r_{18} = 0.68$, $P = 0.001$). However, this correlation waned as time spent foraging with the new companions passed (last food distribution before assortment versus last food distribution used with assorted flocks: $r_{18} = -0.07$, $P = 0.812$).

A comparison of the proportion of patches scrounged by birds ($N = 20$) in the assorted flocks revealed that birds in the scrounger flock scrounged more than birds in other flock types immediately after assortment (estimate ± SE = 0.77 ± 0.33, $Z = 2.34$, $P = 0.019$; Fig. 3a), but these differences did not persist in further food distributions (estimate ± SE = −0.25 ± 0.26, $Z = -0.97$, $P = 0.334$; estimate ± SE = 0.23 ± 0.36, $Z = 0.64$, $P = 0.523$). Overall, assorted flock type (scrounger versus producer and intermediates) was not a significant predictor of the proportion of patches scrounged (estimate ± SE = 0.03 ± 0.16, $Z = 0.19$, $P = 0.852$). Flock types also did not differ in intake rate (each food distribution separately: $F_{2,17} = 0.006$, $P = 0.994$; $F_{2,16} = 0.194$, $P = 0.826$; $F_{2,17} = 0.971$, $P = 0.399$; all distributions: $F_{2,17} = 0.325$, $P = 0.727$; Fig 3b).

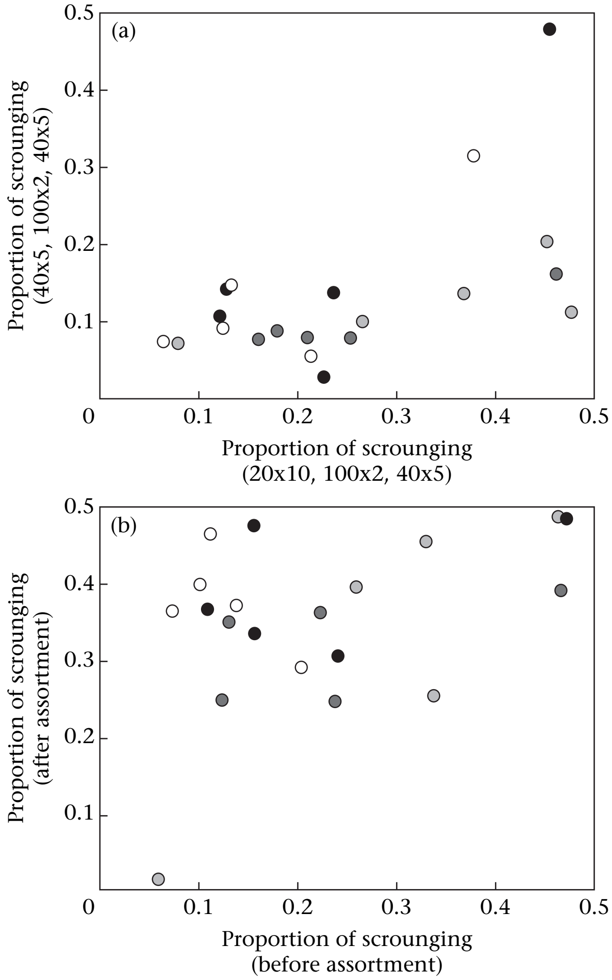

Figure 2. Individual scrounger use (mean proportion of patches scrounged) (a) with the same companions at a 6-month interval: two flocks foraged initially on food distributions 20×10, 100×2, 40×5 and 6 months later on food distributions 40×5, 100×2, 40×5 (open circles and light grey circles), while the two other flocks received food distributions 40×5, 100×2, 40×5 first and 20×10, 100×2, 40×5 6 months later (dark grey circles and closed circles), ($N = 20$); and (b) with different companions before and after assortment (see text for details; different symbols refer to flocks before assortment; $N = 20$).

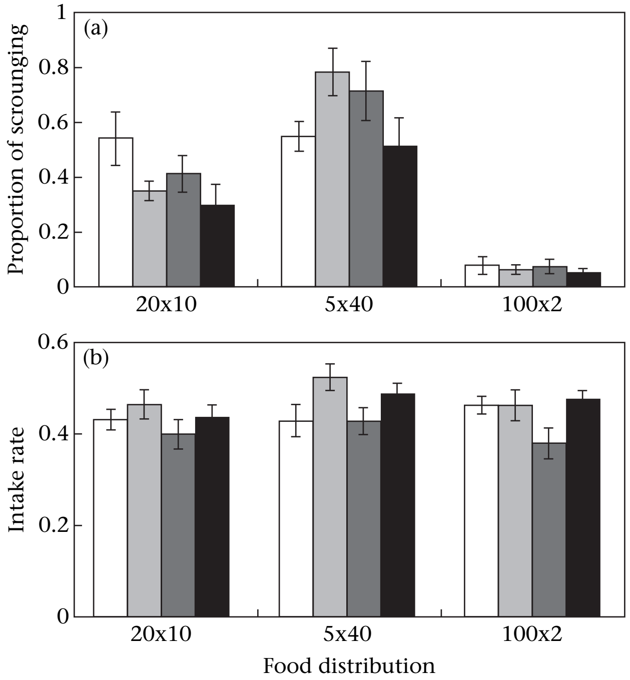

Figure 3. (a) Mean ± SE proportion of patches scrounged by birds and (b) mean ± SE intake rate (seeds/s) in the assorted scrounger (white bars), intermediates (light and dark grey bars) and producer flocks (black bars). All four flocks of five birds foraged in identical food distributions in the following order: (1) 20 patches × 10 seeds; (2) 5 patches × 40 seeds and (3) 100 patches × 2 seeds.

DISCUSSION

Our experiments on nutmeg mannikins revealed significant individual differences in scrounger use that were consistent across different seed distributions and persisted over 6 months. However, both experiments revealed that this consistency could be broken by changing flock composition, thereby rejecting fixed phenotypic or genetic limitations on tactic use. When flocks were formed by assorting birds based on scrounger use, there was no difference in the mean proportion of patches scrounged or in intake rate by birds in the different flock types, suggesting stronger plasticity than consistency effects on tactic use. The mechanism responsible for individual differences must therefore allow for differences to persist only as long as group composition remains unaltered, but decay whenever companions use different combinations of producer and scrounger, forcing individuals to respond by adjusting their tactic use. We discuss the characteristics of such a mechanism below.

One possible mechanism that would meet these characteristics involves the existence of a relative phenotypic limitation on scrounger use that depends on the phenotypes of flockmates. For instance, individuals that behave consistently in one context may exhibit different behavioural responses when tested with different groupmates (Magnhagen & Staffan 2005; Stöwe et al. 2006; Piyapong et al. 2010). In zebra finches, *Taeniopygia guttata*, a closely related social, seed-eating, estrildid finch, Beauchamp (2001) observed a significant correlation in scrounger use when individuals were moved from one flock to another, a result that contrasts with our own. Perhaps there exist important differences in the social organization of these two estrildid finches that can account for this. For instance, Giraldeau et al. (1990) noted that social dominance and sex could play a somewhat stronger role in the PS dynamics of zebra finches than it does in nutmeg mannikins. However, it is difficult to ascertain whether the difference between Beauchamp's (2001) study and our own is attributable to procedural differences in methodology or to ecological differences between the species. Future investigations could test specific hypotheses on relative phenotypic determination of scrounger use (e.g. sex, dominance) by examining the adjustment in scrounger use by focal birds foraging in different flocks with companions of known phenotypes.

The persistent individual differences we report in the current study could also have arisen without any prerequisite underlying intrinsic phenotypic differences (see also Oosten et al. 2010) if individuals allocate behaviour to each tactic according to the payoffs they recently experienced. For instance, when a bird chooses to increase its use of one tactic in response to a recent increase in payoff from that tactic, say producer, it incidentally increases the relative payoff to scrounger for all other group members. If the group members respond to these changed payoffs by altering their use of each tactic, they will also inevitably change the payoffs being experienced by all other companions. If the birds behave in this way, then initial random differences in the success they experienced as producer and scrounger would be amplified by the frequency-dependent feedback (Giraldeau 1984; Giraldeau & Caraco 2000). Once the combination of tactics used within a group happens to correspond to the stable equilibrium frequency (SEF) of scrounger, however, all individuals within the group experience the same payoff from using producer or scrounger tactics, irrespective of the frequency with which they use each. Deviating from their tactic use would then always provide a decreased payoff and so they have no better option than continue playing the assortment of tactics they were playing when the group hit the SEF (Mottley & Giraldeau 2000). Individuals would then keep their allocation unchanged so long as no change in group composition perturbs the payoffs. If we are correct, then the extent to which social groupings are open to changed compositions in the wild may determine the extent to which individual differences acquired from tracking frequency-dependent payoffs will persist or not. This mechanism is also consistent with a phenotypic limitation or behavioural bias that would create initial differences in payoffs for one tactic or the other (e.g. learning ability; Katsnelson et al. 2011), which would then be crystallized through frequency-dependent learning. Long-term persistence of these putative phenotypic limitations could lead individuals to develop similar biases every time they are reassembled with the same companions, thereby explaining long-term consistency of scrounger use within the same flock configuration. However, a previous study could find no association between scrounger use and morphology or personality in nutmeg mannikins (Thibaudeau 2004).

The results of experiment 2 are consistent with a positive feedback loop in the form of frequency-dependent learning based on random or phenotypically constrained individual differences in the payoffs to each tactic among a flock. When birds with high scrounger profiles were placed in the same flock, they initially exhibited higher levels of scrounging than birds in the other flocks, suggesting that birds always start off using the combination of producer and scrounger they had been using consistently in earlier trials. However, after 3 days, the flock was showing scrounging frequencies that were similar to those of flocks composed of intermediate- or low-scrounging individuals because flock type was not a significant predictor of individual scrounger use. A similar temporary carryover effect in scrounger use was observed within stable flocks of nutmeg mannikins responding to a change in seed distribution rather than flockmates (Morand-Ferron & Giraldeau 2010). Animals from various taxa have been shown to adjust scrounger use based on environmental conditions (reviewed in Giraldeau & Dubois 2008), but this is the first demonstration that individuals can also adjust scrounger use in response to a change in the characteristics of companions. This adjustment led assorted flocks to converge quickly to the same SEF values, resulting in similar intake rate among flock types.

Our results suggest that behavioural plasticity can erase idiosyncratic differences in tactic use when individuals are forced to forage with companions with similar tendencies. These results parallel those reported by Magnhagen & Staffan (2005), in which perch, *Perca fluviatilis*, of extreme behavioural types adjusted their behaviour when assorted with individuals of similar boldness. However, in a study on water striders, *Aquarius remigis*, Sih & Watters (2005) found that groups formed of active, hyperaggressive males were still more active than other groups. In water striders, aggressive males have higher fitness than nonaggressive ones (Eldakar et al. 2009); there is thus no incentive for hyperaggressive males to reduce their activity/aggression level after a change in group composition. In the PS game, however, individuals scrounging at a high frequency can increase their payoffs by producing more when the corporate frequency of scrounging exceeds the equilibrium (Giraldeau & Caraco 2000). We might thus expect more behavioural plasticity in response to changes in group composition when payoffs are negatively frequency-dependent, compared with frequency-independent systems; this prediction remains to be explored empirically.

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APPENDIX

Table A1

Treatment (initial, reassembled and assorted) and food distribution (number of patches × number of seeds per patch) for the four flocks used in experiment 2

Duration (days)	Flock treatment and food distribution (patches × seeds)			
	Flock 'a'	Flock 'b'	Flock 'c'*	Flock 'd'*
	Initial	Initial		
8	20×10	40×5		
8	100×2	100×2		
5	20×10	20×10		
	Reassembled	Reassembled	(for assortment)	(for assortment)
8	40×5	20×10	20×10, 100×2	20×10, 100×2
8	100×2	100×2	20×10, 100×2	20×10, 100×2
5	20×10	20×10	20×10	20×10
	Assorted Producer	Assorted Scrounger	Assorted Intermediate	Assorted Intermediate
3	20×10	20×10	20×10	20×10
3	5×40	5×40	5×40	5×40
3	100×2	100×2	100×2	100×2
			Initial	Initial
8			20×10	40×5
8			100×2	100×2
5			20×10	20×10
			Reassembled	Reassembled
8			40×5	20×10
8			100×2	100×2
5			20×10	20×10

Each flock contained five birds.

* After the assorted treatment, flocks 'c' and 'd' were formed into initial flocks using eight of the original birds and two new individuals.