Individual differences in plasticity and sampling when playing behavioural games

Julie Morand-Ferron^{1,2,*}, Elisabeth Varennes¹
and Luc-Alain Giraldeau¹

¹Département des Sciences Biologiques, Université du Québec à Montréal, C.P. 8888, Succ. Centre-ville, Montréal, Québec, Canada H3C 3P8

²Department of Zoology, Edward Grey Institute of Field Ornithology, Oxford University, South Parks Road, Oxford OX1 3PS, UK

When engaged in behavioural games, animals can adjust their use of alternative tactics until groups reach stable equilibria. Recent theory on behavioural plasticity in games predicts that individuals should differ in their plasticity or responsiveness and hence in their degree of behavioural adjustment. Moreover, individuals are predicted to be consistent in their plasticity within and across biological contexts. These predictions have yet to be tested empirically and so we examine the behavioural adjustment of individual nutmeg mannikins (*Lonchura punctulata*), gregarious ground-feeding passerines, when playing two different social foraging games: producer–scrounger (PS) and patch-choice (PC) games. We found: (i) significant individual differences in plasticity and sampling behaviour in each of the two games, (ii) individual differences in sampling behaviour were consistent over different test conditions within a game (PC) and over a six month period (PS), (iii) but neither individual plasticity nor sampling behaviour was correlated from one social foraging game to another. The rate at which birds sampled alternative tactics was positively associated with seed intake in PS trials but negatively associated in PC trials. These results suggest that games with frequency dependence of pay-offs can maintain differences in behavioural plasticity but that an important component of this plasticity is group- and/or context-specific.

Keywords: behavioural reaction norms; ideal free distribution; personality; producer–scrounger game; responsiveness; social foraging

1. INTRODUCTION

The ability to adjust behaviour to current conditions is a form of reversible phenotypic plasticity that has been studied under the optimality framework (e.g. [1]), and more recently by researchers exploring the idea of animal personalities [2,3]. A recent review on ‘behavioural reaction norms’ (BRN; [4]) revealed that individuals of a same population can differ not only in the value of a behavioural trait under specific conditions (elevation of the BRN), but also in the extent to which they can adjust their behaviour over an environmental gradient, or behavioural plasticity (slope of the BRN; but see [5,6]). For instance, Ural owl (*Strix uralensis*) mothers vary in the intensity of nest defence behaviour as well as in the extent to which they adjust aggressiveness in response to variation in food availability [7]. Individual variation in behavioural plasticity has been linked to other aspects of personalities such as proactive versus reactive coping styles [8], activity level [9], and exploration [10]. Why such individual differences in behavioural plasticity should arise and persist is not yet well understood; recent theoretical advances suggest negative frequency dependence of pay-offs to behavioural alternatives as an adaptive explanation [11–13].

In frequency-dependent selection, rare strategies have an advantage over others such that no type can reach

fixation, maintaining variation in the population (reviewed in [14]). This variation can be observed between individuals (e.g. cryptic colorations [15]) or within individuals of a given population (e.g. cooperation versus defection on successive interactions [16]). In behavioural games [17], determinants of evolutionarily stable solutions (ESS; [18]) may change frequently within generations and therefore the ability to respond plastically to environmental variation is often expected to evolve [19–22]. Such plasticity would allow individuals to adjust their use of behavioural tactics to current conditions and state. For example, foragers can track variation in patch quality, approximating an ideal free distribution over the whole habitat [23,24].

Recent models examining the evolution of behavioural plasticity in social foraging games however predict the coexistence of fixed and responsive strategies; i.e. plasticity is not the ESS in all games [11–13]. For instance, in a social patch-choice (PC) game (cf. [23,24]), the ESS is a mixture of responsive animals that select a foraging patch on the basis of its initial quality and unresponsive ones that choose randomly [12]. The mixture is expected when the costs of being responsive are smaller than benefits obtained from tracking the environment. As the responsive strategy spreads, its benefits decrease as more individuals compete within the patch that was initially the best. At some point, the gains from being responsive equal those of choosing randomly and so the responsive strategy can never totally replace an

* Author for correspondence (julie.morand-ferron@zoo.ox.ac.uk).

unresponsive strategy. From this model, we expect individuals to differ in the extent of behavioural adjustment they exhibit in response to changes in environmental conditions. Moreover, if costs to plasticity can be reduced and/or benefits increased over successive behavioural adjustments (e.g. through learning), we expect these individual differences to be consistent within and across biological contexts [12].

Plasticity is also not an ESS when the choice of a tactic is based on the estimation of frequency-dependent pay-offs, for instance in a producer–scrounger (PS) game [13]. In this game, the producer looks for hidden resources while the scrounger exploits the producer's effort [24,25]. Plastic players that decide on their investment on the basis of pay-offs obtained using each tactic can never spread to fixation within a population [13]. This mixture of plastic and non-plastic individuals is stable because the behavioural adjustment of plastic individuals affects the value of the alternatives for all players, hence buffering selective pressures on non-plastic individuals. While plastic individuals can do better than fixed producer or fixed scrounger depending on the conditions, they can never do better than both simultaneously, because their behaviour always favour one of the fixed types, who are therefore never totally replaced by plastic strategists. This model thus also predicts individual differences in plasticity in tactic use.

Very few empirical studies have examined individual variation in behavioural plasticity in a game-theoretical context (see review by Dingemanse *et al.* [4]). In a study on wild Carib grackles (*Quiscalus lugubris*; [26]), individuals seemed to differ in propensity to adjust their use of producer and scrounger foraging tactics in response to experimental manipulation of the cost of producing and scrounging. However, these field observations did not control for contextual variables such as availability of other food sources, group size and composition. Also, the rate at which individuals switch between alternative tactics in social foraging games, and thus the rate at which they potentially obtain information on the value of such alternatives has not been examined yet.

Here we examine the change in the use of alternative foraging tactics in captive, wild-caught individual nutmeg mannikins (*Lonchura punctulata*) in two social foraging games: PS [25] and PC games [23]. In both of these games, the value of the alternatives depends on the behaviour of other players, such that all other things being equal, playing one tactic will be more valuable the fewer individuals are engaged in that tactic. For each game context, we exposed flocks of mannikins to different seed distributions and measured individual adjustment in tactic use over experimental conditions. In the PS game, plasticity should be expressed as an increase in scrounger use with increased number of items per patch, as there are then potentially more items left in the patch upon arrival by the scrounger [27]. In the PC game, plastic individuals should increase their use of a given patch when its richness increases [23]. Because plasticity might require collecting information on the value of different behavioural options [11–13], we also noted the rate at which birds sampled alternative tactics in each game.

We tested the following predictions: (i) individuals differ in behavioural plasticity and sampling behaviour in both games, (ii) individual differences in sampling

frequency are repeatable over time within a game context, and (iii) individual plasticity and sampling rate are correlated between the two games. Finally, we examined whether high or low values for plasticity and sampling rate were favoured in the PS and PC games.

2. MATERIAL AND METHODS

(a) *Subjects and housing*

We randomly selected 20 individuals from our colony of 24 birds to form four flocks (A, B, C and D) of five individuals for PS experiments. Flocks were then adjoined two by two (AB and CD) for the PC experiment. One bird died during the habituation period of the PC experiment; flock size was therefore nine for flock AB and 10 for flock CD. During experiments, each flock was kept in an indoor aviary (1.5 × 3.8 × 2.3 m high) at constant temperature on a 12 L:12 D light cycle. Aviaries were equipped with perches, water dispensers and baths. A one-way mirror allowed the observer to record trials using a video camera from outside the test room.

(b) *Producer–scrounger experiment*

Each aviary was equipped with a foraging grid containing 100 equidistant wells in which white millet seeds could be hidden. All individuals had played PS in previous studies, but never with the current flock compositions. After flocks were formed, birds were allowed to familiarize themselves with the aviary and received unlimited access to a commercial mixture of seeds for a minimum of 5 days. Before each experimental day, birds were food-deprived overnight and for an additional hour after lights on. We conducted one trial per hour, for a total of 10 trials per day, after which birds received ad libitum access to food for 2 h. We observed only one focal bird at each trial. The order of observation of the birds was determined haphazardly with the constraint of observing each bird twice daily, never at the same time of day within 5 consecutive days. A trial started when the observer removed the opaque plastic sheet covering the grid and ended when no new food patch was found for 30 s or after the trial had lasted 5 min, whichever occurred first. If no bird landed on the grid for the first 5 min of a trial, the grid was covered and the trial restarted 5 min later. If the focal bird did not land on the grid within another 5 min, the trial was coded as a missing value ($n = 51$ out of 1680 trials). Also, in order to use only trials where birds showed sufficient motivation to feed, we excluded trials where focal birds ate from two patches or less ($n = 17$ out of 1680 trials).

Each flock went through two experiments, each composed of a succession of three phases of 8, 8 and 5 days, respectively: (i) 10 seeds × 20 wells (for two randomly chosen flocks) or 5 seeds × 40 wells (for the other two flocks), (ii) 2 seeds × 100 wells (all flocks), and (iii) 10 seeds × 20 wells (all flocks). Each phase was followed by a 2 day period during which no trial was conducted and birds had ad libitum access to food. Birds were then returned to randomly selected cages of the colony for a period of six months during which time some birds were used in other experiments, but never with the same flock compositions. After this period, we reunited the flocks and ran a second experiment using the same protocol, but with the food distribution in the first phase reversed for the flocks.

From video files, we noted the number of seeds eaten as a producer (focal bird discovers a new, unoccupied patch) and

as a scrounger (focal bird joins a patch where others are already feeding), as well as the time spent on the foraging grid by focal birds. Tactic use was defined as the proportion of seeds scrounged over total seeds eaten at each trial. To measure sampling behaviour, we noted from video files of the first day of each experiment ($n = 77$ trials) the number of times individuals switched between producing and scrounging a patch within a trial.

(c) Patch-choice experiment

Each aviary was equipped with two identical foraging patches (left and right) located on two tables 50 cm apart. Each patch was equipped with a $36 \times 24 \times 5$ cm glass container receiving seeds from an automated feeder (Med Associates Inc.) modified to be controlled manually from outside the aviary. Feeders were rigged to deliver 2.55 ± 2.9 (mean $\pm$ s.d.) white millet seeds at a time. The rate of delivery was chosen such that in most trials, food items would be consumed immediately as they entered the patch, conforming to a continuous-input PC [24,28]. All birds were naive to this experimental set-up; after flock formation, we provided birds with ad libitum access to a mixture of seeds near their perching area for 3–7 days. We then trained the birds to feed at the two patches by providing a total of 246 seeds on a 1:1 resource ratio at hourly interval four to seven times per day, after 14 h (overnight plus 2 h) of food deprivation. This training period lasted until most (80%) birds would feed simultaneously in patches for a minimum of four sessions per day (flock AB = 4 days; flock CD = 2 days). We then conducted six trials per day over 6 days, with a 2 day break with ad libitum food within this period. Birds received ad libitum access to a commercial seed mixture and ground oyster shells at the end of daily trials, until lights off. Each trial lasted 150 s; in the first 30 s of each trial, three seeds were given every 10 s to attract birds to the patches. In the next 30 s, both feeders were activated on a 1:1 ratio. Data collection began after 60 s and lasted 90 s during which feeders were activated following one of three randomly chosen left:right resource ratios: 1:2, 1:1 and 2:1. We paused in the process whenever all birds flew away from the patches.

We noted the number of seeds eaten and the time spent in each patch (left and right) for all birds at each trial from video playbacks of the trials. In order to use only trials where birds showed sufficient motivation to feed, we excluded data for focal birds that ate fewer than three seeds ($n = 35$ out of 684). Tactic use was defined as the proportion of seeds eaten at the left patch over all seeds eaten in a trial. Sampling behaviour was characterized by noting the number of times a bird travelled between the left and right patch (i.e. arriving to the alternative patch within 10 s) within each trial ($n = 649$ trials).

(d) Statistical analyses

We used a random regression approach [4,29,30] to examine individual differences in behavioural plasticity in tactic use over different experimental conditions (i.e. ‘contextual reaction norms’ [31]). As our dependent variables were proportions (i.e. proportion of seeds scrounged in the PS game, proportion of seeds eaten in the left patch in the PC), we used generalized linear mixed models with a binomial response (using the function ‘glmer’ in R v. 2.10.0 [32]). The response variable was a two-column matrix representing the raw number of ‘successes’ (i.e. seeds eaten as a

scrounger, or at the left patch) and ‘failures’ (i.e. seeds eaten as a producer, or at the right patch; [33]). Full models included mean-centred seed distribution (i.e. number of items per patch or food ratio minus mean value for the sample [4]), day (PC) and time of day as fixed effects. In PS experiments, mean proportion of scrounging was close to zero for all birds in the two-seed food distribution; we thus compared scrounger use in the five- versus 10-seed food distributions when assessing individual differences in tactic use and plasticity. Because previous seed distribution influenced tactic use for some time after changing conditions (cf. [34]), we used data from the last day for each of these distributions ($n = 77$); however, results were similar with the full dataset (not shown). We included whether this experiment was conducted first or second (order) as a fixed effect. For PC analyses, we compared use of the left patch among the two extreme food ratios, 1:2 and 2:1 (similar results were obtained with the full dataset; not shown), and included trial number as an additional random effect to control for the recording of multiple individuals from a same trial ($n = 649$ data points over 72 trials). We ran each model while including and excluding (i) a random intercept for focal bird’s identity, thereby assessing individual differences in tactic use (elevation of the BRN) and (ii) a random slope for identity over experimental conditions, thereby examining individual differences in plasticity in tactic use (slope of the BRN). The likelihood of the models including or excluding each random effect was compared using the function ‘anova (model 1, model 2)’ (log-likelihood ratio test [30,35,36]). We used the absolute value of the difference in mean tactic use between the two food distributions of a game (i.e. the delta Y component of individual slopes) as a measure of individual plasticity ([37]; see [4,31] for alternative operational definitions for plasticity). We then examined whether an individual’s plasticity in scrounger use was associated with its plasticity in left patch use (arcsine-square-root transformed values) using a Pearson’s correlation test.

To examine the statistical significance of differences in the frequency at which individuals switched between alternative tactics, we compared the likelihood of a linear mixed model with versus without focal bird’s identity as a random effect (i.e. with focal within flock versus only flock as a random effect). The likelihood of the models including or excluding this random effect was again compared using the function ‘anova (model 1, model 2)’. The response variable—number of transitions between alternative tactics per trial—was square-root transformed to improve normality [33]. We included relative tactic use and time of day as fixed effects, as well as the number of seconds spent on the foraging grid (PS) or at the two patches (PC) in order to control for the opportunity to express such tactic switches. In the case of the PC game, we also included seed distribution and day as fixed effects, and trial number as a random effect. We used partial correlation tests (controlling for flock) to assess whether individual differences in transition rate (square-root transformed) were consistent across different resource ratios (PC) and over a six month period (PS); this allowed taking into account that individual birds were tested with a fixed set of companions. Because flock composition differed among the two games, we used a Pearson correlation test to examine whether sampling rate correlated across the two games.

Finally, we used linear mixed models to examine the relationship between total seed intake (log-transformed)

Figure 1. Scrounger use (mean proportion of seeds scrounged) by nutmeg mannikins in flocks (a) A, (b) B, (c) C and (d) D ($n = 5$ in each flock), on the last day of observations using five and 10 seeds per patch (experiment used five, two and 10 seeds per patch, successively). The grey dashed line shows mean values for the whole flock for each food distribution.

Table 1. Comparison of generalized linear mixed models differing only in their random structure. (The response variable was the number of seeds scrounged and produced (PS game) or the number of seeds taken from the left and the right patch (PC game). Fixed effects: seed distribution (mean centred), day, time of day (and first versus second experiment for PS models). Additional random effect for all PC models: trial number. 'x' indicates random effects fitted in each model. The significance of difference in model fit is based on log-likelihood tests (significant differences are in bold). FL, flock; ID, identity of focal bird; FD, food distribution; ID * FD, individual slope over food distributions; LRT, χ^2 -value for the log-likelihood ratio test.)

response	FL	ID	ID * FD	model	likelihood	test	LRT	d.f.	<i>p</i>
scrounger use	x			1	-363.6				
	x	x		2	-168.3	1 versus 2	390.7	1	<0.001
	x	x	x	3	-143.1	2 versus 3	50.5	1	<0.001
left patch use	x			1	-3136.8				
	x	x		2	-2536.0	1 versus 2	1201.6	1	<0.001
	x	x	x	3	-2457.5	2 versus 3	157.0	1	<0.001

and number of transitions while controlling for time spent on the grid or patches, tactic use, time of day and day whenever appropriate, with individual nested within flock (and the trial number for the PC) as random factors.

3. RESULTS

(a) Plasticity in alternative tactic use

On average, birds increased their use of the scrounger tactic over the producer tactic when the number of items per patch increased (figure 1; model including a random intercept for flock and for individual: estimate = 0.20 ± 0.02 , $Z = 7.3$, $p < 0.001$). Mixed-model analyses revealed significant individual differences in scrounger use and in adjustment in scrounger use across the two food distributions (table 1). In PC trials, most mannikins increased their use of a patch when its relative richness increased (figure 2; model including a random intercept for flock, individual and trial number: estimate = 0.86 ± 0.05 , $Z = 18.2$, $p < 0.001$). Here again we found significant differences in both individual intercepts and slopes for tactic use over two food distributions (table 1). The correlation between elevation and slope of individual BRN was 0.643 in the PS game and 0.294 in the PC game.

In the PS game, the absolute difference in the proportion of seeds scrounged by individuals in the five-versus 10-seed condition ranged from 0 to 0.529. In the PC game, the absolute difference in the proportion of seeds taken from the left patch between the 1:2 and 2:1 food ratio ranged from 0.006 and 0.615. These values for individual plasticity did not correlate across the two games (figure 3a; $n = 19$, $r = 0.377$, $\chi^2_1 = 2.53$, $p = 0.112$; with extreme data point (0.529, 0.615) removed: $n = 18$, $r = 0.074$, $\chi^2_1 = 0.09$, $p = 0.771$). Because the correlation between individual intercept and slope was quite high in the PS game (0.643), we repeated this analysis controlling for scrounger use; we again found no convincing correlation pattern across the two games (partial correlation controlling for mean scrounger use: $n = 19$, $r = 0.459$, $F_{1,16} = 4.4$, $p = 0.053$; with extreme data point (0.529, 0.615) removed: $n = 19$, $r = 0.25$, $F_{1,15} = 1.0$, $p = 0.331$).

(b) Sampling alternative tactics

Individual differences in the propensity to sample alternative tactics were statistically significant in both games; these differences accounted for 46 per cent of the variance in the

Figure 2. Left patch use (mean proportion of seeds taken from the left patch) by nutmeg mannikins in (a) flocks AB ($n = 9$) and (b) CD ($n = 10$), under left:right resource ratios 1:2 and 2:1. The grey dashed line shows mean values for the whole flock for each food distribution.

Figure 3. Individual values for (a) plasticity (absolute value of the difference in mean proportion of seeds scrounged when patches contained five versus 10 seeds, and in mean proportion of seeds taken from the left patch when food ratio was 1:2 versus 2:1), and (b) sampling rate (number of tactic switches per minute spent on the grid or patches), in the PS versus in the PC game ($n = 19$).

PS game (likelihood ratio test = 11.9; d.f. = 1, $p < 0.001$) and for 32.3 per cent in the PC (likelihood ratio test = 115.6; d.f. = 1, $p < 0.001$). Individual sampling rate was not correlated with tactic use (PS: $n = 20$; $r = 0.376$, $F_{1,15} = 2.5$, $p = 0.137$; PC: $n = 19$; $r = 0.352$, $F_{1,16} =$

Figure 4. Relationship between the number of tactic switches per minute and the number of seeds eaten per minute (a) in PS trials and (b) in PC trials, with linear fit shown.

2.3, $p = 0.153$). In the PS game, individual values for sampling rate were positively correlated between the two experiments conducted at a six month interval (partial correlation controlling for flock: $n = 20$, $r = 0.653$, $F_{1,14} = 10.4$, $p = 0.006$). Mean individual sampling rate was also positively correlated among the three resource ratios in the PC game (partial correlation controlling for flock, left:right ratios 1:1 versus 1:2 and versus 2:1, respectively: $r = 0.848$, 0.790 ; $n = 19$, $F_{2,15} = 23.2$, $p < 0.001$). However, mean individual sampling rate did not correlate across the two games (figure 3b; $n = 19$, $r = 0.100$, $\chi^2_1 = 0.17$, $p = 0.683$).

(c) Plasticity, sampling and intake rate

Individual plasticity values were not correlated with mean intake rate (partial correlation controlling for flock, PS: $n = 20$; $r = -0.284$, $F_{1,15} = 1.1$, $p = 0.269$; PC: $n = 19$; $r = 0.073$, $F_{1,16} = 0.09$, $p = 0.773$). The number of times a bird switched between alternative tactics during a PS trial was positively associated with intake rate during this trial (figure 4a; $F_{1,53} = 6.7$, $p = 0.012$), while this relationship was negative in PC trials (figure 4b; $F_{1,623} = 42.7$, $p < 0.001$).

4. DISCUSSION

Our analyses revealed significant individual differences in tactic use, in behavioural plasticity in tactic use, and in the frequency at which birds sampled alternative tactics in the PS and PC games. These results provide, to our knowledge, the first published empirical evidence of individual differences for behavioural plasticity in a game context. Such individual differences were predicted by at least three theoretical studies on the evolution of plasticity in a

game context [11–13]. However, we did not find evidence for the prediction that individual plasticity would be correlated across the two games [12]. Observed differences in plasticity and in sampling behaviour were found to be game- and/or group-specific.

Individuals differed in the frequency at which they used alternative tactics: in the PS game, some were generally more inclined to scrounge than to produce, while in the PC, some used preferentially one patch over the other. Individual differences in scrounger use have already been described in various taxa (e.g. [38,39]), and biases for a specific patch have been taken into account in PC research [40]. However, most game-theoretical studies have documented mean plastic responses exhibited by social groups, without partitioning plasticity among members of a group. Our results suggest that the group-level plasticity that is predicted by game models [24] is not necessarily the product of similar adjustment by all group members such that foraging groups may be polymorphic in terms of behavioural plasticity. Individuals also differed in the extent of their sampling behaviour in both game contexts, with some birds responding to variable environmental conditions by frequently switching tactics, while others avoided switching and foraged for longer bouts while engaged in the same tactic. Individual differences in sampling behaviour were stable characteristics of individuals and not merely a form of consistency attributable to repeated measurements taken over short intervals (cf. [41]). This is particularly true in the PS game where these individual differences persisted over six months. This persistent intraspecific variation might thus correspond to personality differences that have been associated with a trade-off between exploitation and exploration [11] and in responsiveness to external stimuli [8,12,42].

In contrast with predictions from Wolf *et al.* [12], neither individual plasticity nor sampling rate was correlated among the two games. While the consistency of individual differences in sampling behaviour within a game might have been owing to positive feedback effects reducing the costs of sampling or increasing its benefits over repeated trials (e.g. learning to use information more efficiently [2,12]), such feedback effects did not seem to operate between games. Because the size and composition of flocks differed between PS and PC games, it is also possible that the lack of correlation in individual plasticity and sampling rate between the two games was owing to different behavioural adjustment by mannikins to flock members. Because we used the number of seeds obtained using each tactic rather than investment *per se*, it is possible that observed individual tendencies were somewhat constrained by the behaviour of different companions; for instance, a seed can only be scrounged when patches are produced by others. However, we do not expect this to have had a significant effect on the conclusions of our study, as earlier work demonstrated that investment measured as the effort placed in hopping with the head up for scrounger and with the head pointing down for producer changes in parallel with joining and finding patches, respectively [43].

Our examination of the relationship between plasticity and seed intake revealed no association between

individual values for relative plasticity and mean intake rate, suggesting that the different plasticity types represent equivalent alternatives in terms of pay-offs, as would be expected at the ESS [12,13]. A finer grained analysis at the level of trials on the relationship between sampling behaviour and seed intake revealed that in PS trials, a higher sampling rate was associated with an increased rate of seed consumption, while the opposite was true for PC trials. It thus seems that alternating between producing and scrounging implied low costs and/or high benefits, while travelling between left and right patches—despite the patches being located very close to each other—was overall more costly. Because of differences in costs and benefits to sampling behaviour in the two games, skills or knowledge gained from behavioural adjustment in PS trials might not have been applicable to the PC, potentially leading each bird to reassess anew its investment in exploration versus exploitation in each game. This suggests that there are no strong phenotypic determinants of sampling behaviour or that these determinants are group and/or context dependent, thereby explaining the absence of correlation in sampling rate between the two games.

It is not known to what extent the individual differences observed in this study are linked to a potential genetic polymorphism. It seems likely that a mixture of individuals expressing different levels of plasticity could just as well be obtained solely on the basis of decision-making and frequency dependence of pay-offs, with behavioural adjustment by some individuals buffering others against changes in pay-offs that would normally occur when the environment changes. That behavioural processes reach the same outcomes as natural selection acting on genetic alternatives is commonly assumed in behavioural ecology and corresponds to what Giraldeau & Dubois [22] call the behavioural gambit. Long-term stability of these individual differences could then be owing to some form of positive feedback, reducing the costs and/or increasing the benefits of plasticity over time [2,12]. Further studies could explore the idea of constraints on expressed plasticity levels by re-assorting individuals according to their plasticity and exposing these new groups to varying environmental conditions within a same game: if new groups formed of highly plastic individuals persistently reach new equilibria faster than groups composed of individuals with low levels of plasticity, it would suggest that individuals are not free to express any level of behavioural plasticity and that their decisions concerning plasticity are constrained in some way by their phenotype.

Individual differences in behavioural plasticity have been documented in other biological contexts, including dispersal, anti-predation, aggression and parental care (reviewed in [4]). The causes and consequences of this variation have however just begun to be examined. In foraging games such as the PC, a mixed ESS for plasticity in habitat selection should result in some individuals settling on a patch despite it not being the best option available in the environment. Depending on whether adjustment by plastic individuals is then sufficient to restore an equilibrium distribution in the population or not, such individual differences in behavioural plasticity are liable to result in undermatching, i.e. underuse of the best patches and overuse of the worst ones, a

phenomenon observed in many PC studies [24,40]. Clearly, however, our study supports the expectation that frequency-dependent contexts will promote the existence of individual differences in plasticity within groups. The study of the partitioning of behavioural plasticity among group members might thus provide a method to explore the generality of plasticity polymorphisms.

This study was conducted under protocols no. 600 and no. R1-600 for animal use at UQAM.

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