

Group size effect in nutmeg mannikin: between-individuals behavioral differences but same plasticity

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When group size increases, animals from a wide range of taxa reduce vigilance and increase feeding rate, the so-called group size effect. This effect requires that group members display plastic behavioral responses both in terms of vigilance and foraging to obtain the security benefit from grouping and/or to cope with feeding competition. Most studies on group size effects have reported mean group changes in behavior. However, individuals' adjustment of behavior and thus their individual contribution to the overall group-level plasticity remain unexplored. Using wild-caught nutmeg mannikins (*Lonchura punctulata*), small estrildid finches known to exhibit the group size effect, we investigated individual differences in baseline levels and in plasticity of vigilance and feeding behavior. We experimentally manipulated the number of companions foraging with focal birds and noted how they individually adjusted their vigilance and foraging behavior when group size varied. We found that individuals differed consistently in their vigilance level and foraging rate but not in their ability to adjust to experimental variation in group size. Effect sizes for individual consistency in behavior were as large as those for group-level plasticity. Our results reveal high, albeit not maximal, levels of plasticity in both vigilance and feeding behavior for all individuals in this social foraging context. *Key words:* behavioral consistency, behavioral plasticity, group size effect, nutmeg mannikins, *Lonchura punctulata*, social foraging. [*Behav Ecol*]

Increased foraging group size is a decline of individual level of vigilance coupled with an increased foraging rate: the group size effect (Lima 1995; Lima et al. 1999). This group size effect can be explained by the increased safety occurring in larger groups due to a better efficiency of predator detection (the "many eyes hypothesis"; Lima 1995) and by the numerical dilution of risk provided by the nearby presence of other group members (Pulliam 1973; Caro 2005). This increased safety allows group-living animals to reallocate time saved in vigilance to alternative fitness-enhancing activities like foraging, thereby explaining the higher foraging rates commonly reported in large groups. An alternative explanation for the group size effect is that increasing group size increases competition and so individuals respond by increasing their foraging rates at the expense of vigilance and optimal food-handling time (Clark and Mangel 1986; Beauchamp 2003; Rieucou and Giraldeau 2009). Whatever the explanation, the group size effect has been described for many species (e.g., Elgar 1989; Roberts 1996; Lima et al. 1999; but see Robinette and Ha 2001; Barbosa 2002).

The group size effect requires that individuals display plastic behavioral responses both in terms of vigilance and foraging speed to changes in group size. Such plastic responses might imply costs for the development and maintenance of required

cognitive and sensory structures for plasticity and in gathering information for decision making (DeWitt et al. 1998). Behavioral consistency (i.e., the tendency for different individuals to rank consistently relative to others) can be favored whenever limited individual plasticity is sufficient to cope with environmental changes, thereby minimizing the costs of behavioral plasticity (Sih et al. 2004). In species exhibiting the group size effect, the costs of behavioral plasticity seem to be a price worth paying to gain safety benefits of grouping and/or to respond adequately to increasing competition for the resource (e.g., by foraging more intensely when the number of competitor increases). However, although an individual may modulate its behavioral decisions to cope with different situations, it might still show consistent level of its behavioral responses relative to the responses of other individuals (Johnson and Sih 2007). Because most studies on the group size effect have focused on mean group changes in behavior, it is unknown whether 1) individuals differ consistently in their investment in antipredatory vigilance and/or foraging behavior and 2) whether all individuals display equally plastic responses to changes in group size. To complete the examination of the mean plastic response exhibited by groups of foragers, it will thus require an investigation of the contribution of individual group members to the overall level of vigilance and to the overall group-level plasticity (i.e., the mean behavioral changes observed at the group level).

In a recent meta-analysis of the group size effect in birds, Beauchamp (2008) reported considerable variability in the magnitude of the group size effect either among or within species. Reports of differential investment in antipredatory vigilance and feeding behavior depending on sex (Fitzgibbon 1990; Lung and Childress 2007; Pays and Jarman 2008), life history (Rieucou and Martin 2008), or personality type (Quinn and Creswell 2005) of individuals suggest that

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individual differences might underlie some of the unexplained within-species variation in the magnitude of the group size effect. From what is currently known on the group size effect, we can expect a group-level plasticity in response to variation in group size combined, however, with between-individuals differences in vigilance level and foraging speed. Although previous studies in other biological contexts have reported such a pattern of consistency and plasticity (e.g., Beauchamp 2001), it has proven difficult to compare the strength of these 2 effects. Recently, Briffa et al. (2008) presented a novel statistical framework allowing such a comparison and reported strong consistency but weak plasticity in antipredatory behavior of solitary hermit crabs (*Pagurus bernhardus*).

In this study, we investigated how wild-caught captive nutmeg mannikins (*Lonchura punctulata*), small estrildid finches from Southeast Asia, individually adjust their vigilance and foraging behavior when group size increased. These social granivorous birds usually search for seeds on the ground and show little aggression when feeding in groups (Giraldeau et al. 1990). The group size effect has been previously reported in this species: on average, focal birds increased their foraging rates and lowered their scans in response to an increasing group size (Rieucou and Giraldeau 2009). Here, we examined: 1) whether focal nutmeg mannikins adopted consistent levels of vigilance and feeding rate and 2) whether or not individuals exhibited similar plasticity in their response to group size. After assessing plasticity and consistency in our experimental birds, we compared the strength of these effects following the method of Briffa et al. (2008).

MATERIALS AND METHODS

We analyzed data collected from 23 wild-caught 2-year-old unsexed adult nutmeg mannikins purchased from a commercial supplier. All birds were caged in groups of 4 in the Université du Québec à Montréal animal care facilities at room temperature and under a 12-h day/night lighting regime with ad libitum mix of millet seeds and water. All birds were experimentally naive before this study.

Apparatus

The experimental apparatus consisted of 2 boxes, A and B (18 × 13 × 15 cm), placed 30 cm from each other, equipped with a perch, a drinking trough, and a feeder. Each box had a transparent long side in order to see the birds inside and a short transparent side that allowed the birds inside the box to see birds in the adjacent box. The behavior of a focal bird in box A was recorded by a digital mini DV camera (Canon Optura 30, Canon Canada Inc., Mississauga, Ontario, Canada) from behind a 1-way mirror.

Six birds were randomly (here and thereafter using random tables) chosen and used as experimental subjects. These focal birds were housed together in a cage for 6 days before the beginning of the trials. The rest of the birds were housed in similar conditions and were used to form companion groups. Both focal and companion birds were food deprived overnight plus 2 h after the lights had turned on for a total deprivation period of 14 h before the first trial of a day and then for 90 min between consecutive trials within a day. This allowed us to ensure that all focal and companion birds were in a similar hunger state.

Focal birds were first allowed to get used to experimental conditions by placing each bird alone in box A 4 times a day for 2 consecutive days. The box had a feeder filled with the bird's usual mix of millet seeds. The bird was considered trained when it started eating within 30 s on being introduced into the box. We allowed companion birds to get used to experimental conditions in box B using the same procedure. The

location of the 2 feeders constrained birds to land on the side facing the other box. Consequently, each focal bird foraged at the same distance from companions, which stood aligned on one side of the feeder.

A trial consisted of a foraging session lasting a maximum of 6 min, which started once the focal bird landed on the feeder and ended when it either leaved or stopped foraging for 30 consecutive seconds. Each focal bird randomly experienced each group size of 0, 1, 3, and 5 companions twice. The identity of companions forming the foraging group was randomly chosen before each trial.

We quantified foraging and scanning behavior using Observer 5.0 (Noldus Information Technology, Wageningen, The Netherlands) from video recordings of the trials. We calculated the feeding rate of focal birds as the number of seeds eaten per minute during a foraging session. A seed was considered eaten when after being pecked and manipulated to remove its husk, the focal bird swallowed it. To distinguish between vigilant and nonvigilant behavior, we used the birds' head orientation in the vertical plane. As granivorous birds can visually scan their environment while handling seeds in a head-up posture, we used the part of the vigilance that is related to food handling: the food-handling scan (Lima et al. 1999; Fernandez-Juricic et al. 2004). Changes in food-handling scan durations are expected to reflect the role of scramble competition for food resources (Clark and Mangel 1986; Beauchamp and Livoreil 1997; Lima et al. 1999). A bird was considered vigilant while handling a seed in a head-up posture until the seed was swallowed (Figure 1). We calculated the mean food-handling scan duration of a focal bird as the mean duration of all its food-handling scans during a trial.

Statistical analysis

We conducted repeated measures analyses of variance (ANOVAs) using SPSS 10 (SPSS Inc., Chicago, IL) to examine the effect of group size on focal birds' feeding rates and food-handling scan durations. All focal birds experienced each combination of 2 fixed within-subject factors treatments: group sizes (0, 1, 3, and 5 companions) and replicates (2 for each group size). Thus, our analysis was conducted with the mean values of each variables of a focal bird tested for a given group size. We controlled for sphericity for conditions with more than 2 factors using a Mauchly's test. If the sphericity assumption was violated, we used adjusted *P* values after a Huynh and Feldt correction.

To investigate whether focal birds differed in their behavioral responses to variation in group size (thereby exploring differences in individual intercept), we compared 2 general linear models both containing group size (here and thereafter coded as categorical variables to avoid any problem arising from the nonlinearity of the group size series) and replicate as fixed effects, with one including identity of the focal individual as a random effect and one where the random effect was excluded. This comparison allowed us to test for the significance

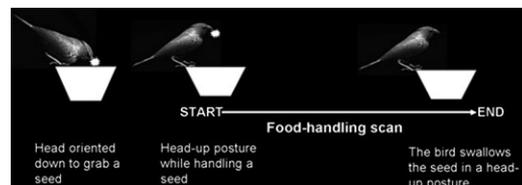


Figure 1

A food-handling scan is defined by the part of the vigilance that is related to food handling. A bird is considered vigilant while handling a seed in a head-up posture until the seed was swallowed.

of between-individuals differences in behavioral responses (Pinheiro and Bates 2000; Martin and Réale 2008). Repeatability estimates (i.e., the fraction of behavioral variation that is due to differences between individuals; Bell et al. 2009) were calculated from the model, including identity of the focal individual as a random effect using the ratio of the variance component related to the random effect (V_i) on the sum of the V_i and the residual variance (V_r) (Pinheiro and Bates 2000; Bell et al. 2009). We conducted model comparison analyses using the `lme` function from the `nlme` package in R 2.3.1 (R Development Core Team 2006) that allows comparing models where one does not include a random effect.

To test for interindividual variation in plasticity of behavioral responses when group size varied (i.e., individual slopes), we compared a model with an interaction between group size and focal birds' identity as a random effect with a model containing only the focal birds' identity as a random effect. This model comparison was performed with the `lmer` function in R 2.3.1 (from the `lme4` package).

We investigated the effect of adding one random effect to a model with a log-likelihood ratio test (Pinheiro and Bates 2000). This test compares the difference multiplied by 2 of log likelihood of the model with the largest number of random effects (model 1) with the log likelihood of the model including the smallest number of random effects (model 2):

Log-likelihood ratio test

$$= 2[\log\text{-likelihood of model 1} - \log\text{-likelihood of model 2}].$$

Finally, we compared the strength of plasticity and consistency based on a quantitative comparison of the effect size estimates (scaling from 0 to 1) for individual consistency and behavioral plasticity when group size increased (see Briffa et al. 2008). We compared the effect size estimates for tests of differences (behavioral plasticity) and tests of consistency between situations. The effect size estimate for behavioral plasticity, η_p^2 (estimating the proportion of variance in responses due to treatment), and the F ratio associated with this analysis were obtained from our repeated measures ANOVA. An effect size estimate equal to zero suggests that the variance in response is not due to the effect of the treatment. Conversely, an effect size estimate equal to 1 indicates that all the variance is due to the effect of the treatment. On the other hand, the effect size estimate for individual consistency was obtained from a nonparametric test of concordance giving the Kendall's coefficient of concordance, W , and its associated χ^2 statistic. The Kendall's coefficient of concordance compares the level of agreement between individual ranks: W equals 0 suggests an absence of agreement between ranks of expressions of behavior (absence of consistent ranking between situations), whereas W equals 1 indicates consistent ranking between situations. For further information about this statistical method, see supplementary material of Briffa et al. (2008). These analyses were conducted in SPSS 10.

RESULTS

Average effects induced by an increased group size

Focal birds showed the commonly reported group size effect (Figure 2). When group size increased, birds increased their feeding rates ($F_{3,15} = 37.47$, $P < 0.001$), whereas they reduced their food-handling scan durations ($F_{3,15} = 13.44$, $P < 0.001$). Neither the replicate (feeding: $F_{1,5} = 1.87$, $P = 0.23$ and vigilance: $F_{1,5} = 0.79$, $P = 0.41$) nor the interaction between group size and replicate were significant (feeding: $F_{3,15} = 2.10$, $P = 0.14$ and vigilance: $F_{3,15} = 1.58$, $P = 0.23$).

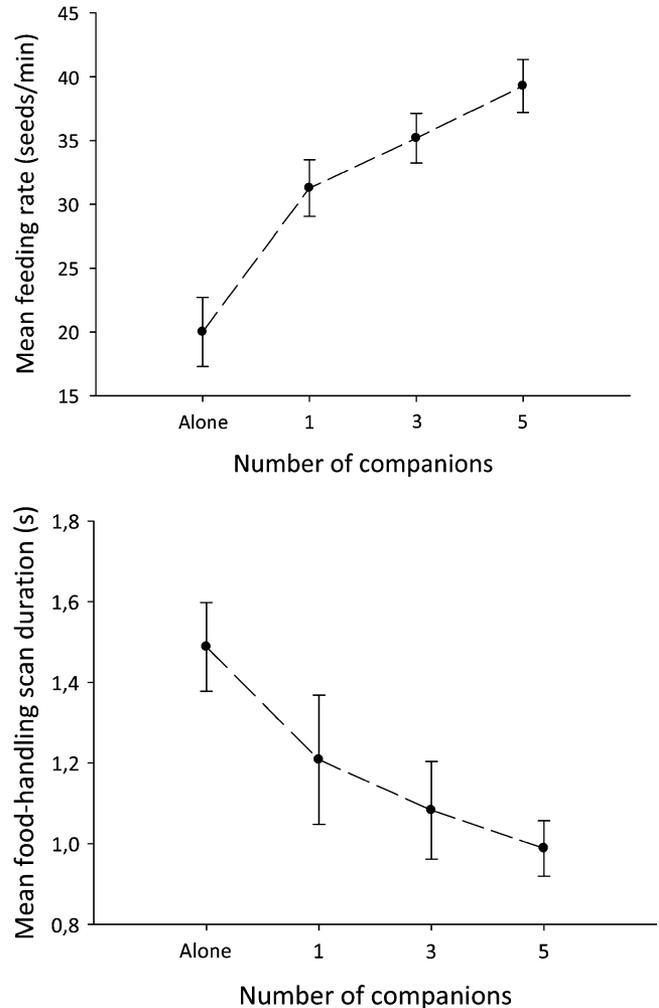


Figure 2

Variation of food-handling scan duration and feeding rate of focal nutmeg mannikins as a function of group size ($N = 6$). All the results are expressed as a mean and its associated standard error.

Individual responses to an increased group size

The addition of identity of focal birds as a random effect in the model significantly improved its fit compared with a model excluding identity as a random effect for both feeding rates and food-handling scan durations (Table 1). Together with the repeatability estimates for feeding rates (0.44) and food-handling scan durations (0.59), our results suggest that focal birds expressed a high level of individual consistency for both vigilance and foraging behavior (Figure 3).

Including an interaction between the identity of focal birds and group size as a random effect in the model did not improve the fit compared with a model including only the identity of birds as a random effect for feeding rates and neither for food-handling scan durations (Table 1). Focal birds therefore adjusted their feeding rates and scans in a similar way when group size was experimentally manipulated (Figure 3).

Consistency versus plasticity

When group size increased, focal individuals were consistent in their feeding rates ($W = 0.795$, $P < 0.0001$) and food-handling scan durations ($W = 0.500$, $P < 0.004$). We conducted a repeated measures ANOVA first on the model containing an interaction between group size and replicate. Because this

Table 1

Comparisons of general linear models (with group size and replicate as fixed effects) with different random factors for feeding rate and food-handling scan duration based on log-likelihood ratio tests: 1) comparison of a model including the identity of the focal individual (ID) as a random effect and one where ID was excluded (difference in individual behavioral responses) and 2) comparison of a model with an interaction between group size and ID as a random effect with a model with only ID as a random effect (interindividual variation in plasticity)

	Log-likelihood	df	Model comparison	Log-likelihood ratio test	<i>P</i>
Feeding rate					
Model 1: without ID	-153.79	5	Model 2 vs. model 1	13.84	<0.0001
Model 2: with ID	-146.87	6			
Food-handling scan duration					
Model 1: without ID	-20.38	5	Model 2 vs. model 1	24.46	<0.0001
Model 2: with ID	-8.14	6			
	Log-likelihood	df	Model comparison	χ^2	$P > \chi^2$
Feeding rate					
Model 2: with ID	-150.37	6	Model 3 vs. model 1	0.0871	0.95
Model 3: with ID × group size	-150.33	8			
Food-handling scan duration					
Model 2: with ID	0.819	6	Model 3 vs. model 1	2.2615	0.32
Model 3: with ID × group size	1.95	8			

df, degrees of freedom. Significant differences between models are in bold.

interaction was not significant, we repeated our analysis on a simpler model containing only group size as the main effect. Effect size estimates for behavioral plasticity in feeding rates ($\eta_p^2 = 0.882$, F ratio = 37.47, $P < 0.0001$) and food-handling scan durations ($\eta_p^2 = 0.729$, F ratio = 13.435, $P < 0.0001$) did not differ largely from those for individual consistency in behavior (feeding rates: $W = 0.795$ vs. $\eta_p^2 = 0.882$ and vigilance: $W = 0.500$ vs. $\eta_p^2 = 0.729$).

DISCUSSION

In this study, we investigated individual contribution to the overall group-level plasticity underlying the well-known group size in a socially foraging passerine: the nutmeg mannikin. Focal birds exhibited consistent individual differences in their level of vigilance and foraging rate but exhibited similar behavioral plasticity when group size changed. We provide here the first statistical comparison of the strength of plasticity and consistency in the feeding and vigilance responses to experimental manipulations of group size. Our results did not reveal strong difference between those large effect sizes. This suggests that both plasticity and individual consistency were important in triggering the observed group size effect in these social birds.

Focal nutmeg mannikins consistently differed from each other in their feeding rate and food-handling scan duration. This conclusion stems from 1) significant differences in individual intercepts, 2) significant rank order consistency in behavior, and 3) from the absence of a significant interaction between group size and replicate. Here, we did not investigate further the potential causes of these individual differences (e.g., sex: Fitzgibbon 1990; Beani and Dessi-Fulgheri 1998; Artiss et al. 1999; Lung and Childress 2007; Pays and Jarman 2008; life history: Forslund 1993; Rieucan and Martin 2008; hunger state: Lima 1995; personality type: Quinn and Creswell 2005) as our main interest was in the consequences of these individual differences and in the balance between individual consistency and plasticity generating the observed group-level response. We discuss our results in relation to these 2 points below.

Interindividual differences in vigilance and foraging point to group composition as an important feature influencing the costs and benefits of group living (see also Dyer et al. 2009). A possible consequence of individual differences in feeding and vigilance behavior is that the overall probability of detecting an approaching predator and/or the overall level of food

competition might be influenced not only by the number of companions in the group but also by whom these companions are and how they behave. Animals might thus need to monitor the vigilance state of their neighbors in order to adjust their own behavior accordingly. There is evidence that some animals, including nutmeg mannikins (Rieucan and Giraldeau 2009), are indeed sensitive to the vigilance state of their neighbors (Fernandez-Juricic et al. 2004). Consequently, vigilance can serve another functional purpose: the acquisition of visual information about social status (Lung and Childress 2007), vigilance levels (Fernandez-Juricic et al. 2004, 2005), or foraging activities (Valone 1989; Shrader et al. 2007) of companions. Another possible consequence of these consistent differences is that individuals might decide which foraging group to join depending on the combination of individuals that are present in those groups; these possibilities remain to be explored empirically.

Feeding and vigilance behavior were repeatable and consistent in our focal birds. This might imply limited individual behavioral plasticity despite an overall group-level adjustment because individuals were not free to adopt all possible values for vigilance and foraging behavior when group size varied (i.e., some individuals were consistently feeding at higher rates, whereas others were consistently more vigilant than others) (Sih et al. 2004; Martin and Réale 2008). Group living is thought to improve safety from predators while allowing animals to redirect effort saved from predator detection toward foraging. If individual consistency in behavior results in an inability to adopt optimal vigilance and feeding patterns at all group sizes, then this consistency may prevent animals from gaining full advantages of grouping. For instance, when in large aggregations where risk dilution rather than early detection provides the main antipredator protection (Dehn 1990), high-vigilance individuals might not effectively reduce scanning effort and would therefore gain lower feeding benefits than low-vigilance or optimally plastic individuals. Conversely, at small group sizes, low-vigilance individuals would face higher predation risk than high-vigilance or optimally plastic individuals. It would thus be interesting to determine whether these limits on plasticity come at a feeding and/or safety cost, and if it is the case, to determine why individuals do not exhibit optimal plasticity.

Recently, Wolf et al. (2008) developed a model predicting that responsive and unresponsive individuals should coexist

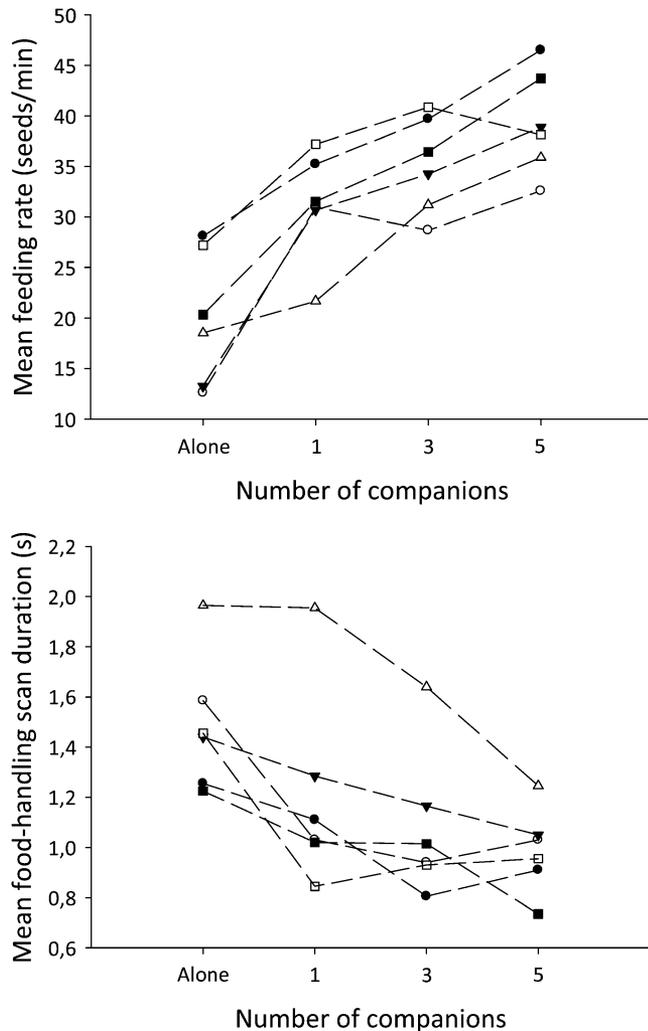


Figure 3 Individual variation of food-handling scan duration and feeding rate of each focal nutmeg mannikin as a function of group size ($N = 6$). Each line represents an individual response.

when payoffs to behavioral plasticity are frequency dependent. Our results do not seem to support this prediction as all individuals were responsive and adjusted feeding and vigilance behaviors to variation in group size. However, although the safety and feeding benefits obtained through group foraging are likely to depend on the behavior of companions, it is not known whether the payoffs to plasticity itself are frequency dependent, with plastic individuals faring better than unresponsive ones when they are rare but as good or worst when common, as required in the model of Wolf et al. (2008).

In an investigation of antipredator responses of hermit crabs, Briffa et al. (2008) found individual consistency in duration of startle responses to be much higher than plasticity across contexts. For social foragers, high levels of plasticity in the feeding/antipredator vigilance trade-off might be favored because although an individual spends time being vigilant, the resource is being consumed by competitors. There is thus an additional cost to vigilance for social foragers that might not apply to solitary foragers for whom the costs of antipredation behavior only translate in loss of feeding time. Further examination of the elevation and slope of individual behavioral response to an environmental gradient (e.g., Nussey

et al. 2007) combined with the method from Briffa et al. (2008) would allow assessing ecological contexts where plasticity has evolved to be weaker, equally strong, or stronger than individual consistency.

Here, we demonstrated that despite strong and consistent interindividual differences, nutmeg mannikins exhibited similar patterns of behavioral plasticity in the group size effect. Previous studies using nutmeg mannikins have shown that the group size effect was triggered by resource competition (Rieucou and Giraldeau 2009). Together with our results showing similar effect sizes for plasticity and consistency of individual vigilance and feeding behaviors, these results suggest that the cost of behavioral plasticity is a price worth paying to respond adequately to increased competition for resource when the number of competitors increases. We encourage researchers to pursue the exploration of the trade-off between behavioral plasticity and individual consistency in other social contexts (Réale and Dingemanse, 2010).

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