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Cognition and covariance in the producer-scrounger game

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ABSTRACT

1. The producer-scrounger game is a key element of foraging ecology in many systems. Producing and scrounging typically covary negatively, but partitioning this covariance into contributions of individual plasticity and consistent between individual differences is key to understanding population level consequences of foraging strategies. Furthermore, little is known about the role cognition plays in the producer-scrounger game.

2. We investigated the role of cognition in these alternative foraging tactics in wild mixed-species flocks of great tits and blue tits, using a production learning task in which we measured individuals' speed of learning to visit the single feeder in an array that would provide them with a food reward. We also quantified the proportion of individuals' feeds that were scrounges ('proportion scrounged'); scrounging was possible if individuals visited immediately after a previous rewarded visitor. Three learning experiments – initial and two reversal learning – enabled us to estimate the repeatability and covariance of each foraging behaviour.

3. First, we examined whether individuals learned to improve their scrounging success (i.e. whether they actually obtained food by scrounging when there was an opportunity to do so). Second, we quantified the repeatability of proportion scrounged, and asked whether proportion scrounged affected production learning speed among individuals. Third, we used multivariate analyses to partition within- and among-individual components of covariance between proportion scrounged and production learning speed.

4. Individuals improved their scrounging success over time. Birds with a greater proportion scrounged took longer to learn their own rewarding feeder. Although multivariate analyses showed that covariance between proportion scrounged and learning speed was driven primarily by within-individual variation, that is, by behavioural plasticity, among-individual differences also played a role for blue tits.

5. This is the first demonstration of a cognitive trait influencing producing and scrounging in the same wild system, highlighting the importance of cognition in the use of alternative resource acquisition tactics. The results of our covariance analyses suggest the potential for genetic differences in allocation to

47 alternative foraging tactics, which are likely species and system dependent. They also point to the need to
48 control for different foraging tactics when studying individual cognition in the wild.
49
50 Key words: alternative tactics, field experiment, individual differences, learning, repeatability, social
51 foraging
52

INTRODUCTION

Multiple tactics can be used by individuals foraging in social groups. Individuals can act as producers, obtaining food directly from the environment, or as scroungers, by taking some share of the food discovered by others (Barnard & Sibly, 1981). Within populations, individuals vary in the extent to which they act as scroungers or producers (Giraldeau & Dubois, 2008). This variation has important ecological consequences because the composition of producers and scroungers in a group influences the spread of innovations, the efficiency of group foraging, and population dynamics (Coolen, Giraldeau, & Vickery, 2007; Giraldeau, Caraco, & Valone, 1994; Giraldeau & Lefebvre, 1987). Although it is well-established that there is negative covariance between the expression of producing and scrounging tactics (Barnard & Sibly, 1981; Beauchamp, 2001; Giraldeau, Soos, & Beauchamp, 1994; Mottley & Giraldeau, 2000), it is unknown whether this covariance arises primarily due to covariance within individuals, for instance due to context-dependent plasticity in tactic expression, or among individuals, due to relatively fixed differences that facilitate the performance of one tactic or the other. The distinction is important, because, notwithstanding the theoretical possibility that individual plasticity (reaction norms) itself might vary in slope among individuals and have a genetic basis, it is primarily the among-individual variance component that indicates the potential for genetic covariance between the two behaviours, and therefore the potential for a correlated response to natural selection on foraging behaviour (Dingemanse & Dochtermann, 2013; Nussey, Wilson, & Brommer, 2007; Wilson et al., 2010).

To understand the factors that generate covariance between producing and scrounging, we must also understand how variance within each behaviour is generated. Cognitive abilities such as learning likely make a substantial contribution to individual variation in foraging behaviours. It has been demonstrated that obtaining food as a producer can require individuals to learn to acquire or process food in novel ways (Laland & Reader, 1999; Ramsey, Bastian, & van Schaik, 2007; Reader & Laland, 2001). In contrast, cognitive mechanisms of scrounging behaviour have received less attention, except perhaps in the specific

context of cache pilfering (Dally, Clayton, & Emery, 2006). Learning could improve scroungers' performance in various contexts, for instance via better recognition and exploitation of opportunities to scrounge (Katsnelson, Motro, Feldman, & Lotem, 2008). Morand-Ferron and Giraldeau (2010) demonstrated a role for learning in adjusting the relative use of producer and scrounger tactics in response to changing environments, and Firth et al. (2015) observed an increase in the frequency of scrounging over days in great tits foraging with their mate at a feeder that was prohibited to themselves. These studies focus on the probability of an individual exhibiting scrounging; however, to our knowledge there are no empirical studies demonstrating that learning is involved in improving the efficiency of scrounging behaviours in terms of the likelihood of an individual actually gaining access to food by scrounging when it has the opportunity to do so. This is an important oversight, because scrounging efficiency could impact overall feeding rates and ultimately survival and fitness. Moreover, many recent studies of cognition in wild populations aim to quantify individual learning (Reichert et al., 2020; Sonnenberg, Branch, Pitera, Bridge, & Pravosudov, 2019), but interpretation of these data may be confounded if scrounging is also a learned behaviour. For instance, estimates of repeatability of production learning speed (Cauchoix et al., 2018) may be overestimated if environmental conditions offer increased opportunities to scrounge, leading to trade-offs due to increased learning of scrounging tactics at the expense of production learning (Beauchamp & Kacelnik, 1991; Fragaszy & Visalberghi, 1989; Lefebvre & Helder, 1997). Thus, considering scrounging and producing simultaneously will enhance the understanding of the cognitive ecology of foraging in wild populations, which is emerging as a major driver of fitness and population-level processes (Shaw, MacKinlay, Clayton, & Burns, 2019; Sonnenberg et al., 2019).

We studied producing and scrounging in mixed-species foraging flocks of great tits (*Parus major*) and blue tits (*Cyanistes caeruleus*). Individuals in these species flock together in the winter and move about woodlands in search of food (Gosler, 1993). They readily use feeders and participate in cognitive assays of foraging behaviour in the wild (Cauchoix, Hermer, Chaine, & Morand-Ferron, 2017; Firth et al., 2015; Morand-Ferron, Hamblin, Cole, Aplin, & Quinn, 2015). We used Radio-Frequency Identification (RFID)

105 controlled feeding stations in which each feeder was programmed to open and allow access to food only
106 to certain individuals based on their RFID, and individuals had to learn which one of the five feeders in
107 the array they were assigned to, in order to measure individuals' production learning speeds in an
108 associative (discriminant) learning task (Reichert et al., 2020). Scrounging was possible in this
109 experimental set-up if individuals visited one of their non-rewarding RFID-controlled feeders very
110 quickly after another individual obtained a reward, because the feeder door remained open briefly
111 (approximately 1 s) after rewarded visits (Firth et al., 2015). Here, we examined producer-scrounging
112 behaviour during a production learning experiment and two reversal production-learning experiments to
113 address the following questions: 1. Do individuals become more successful in scrounging over time (i.e.
114 were visits more likely to result in food obtained by scrounging with increasing opportunities to
115 scrounge), suggesting that they learn to scrounge? 2. Does the proportion of an individual's feeds that
116 come from scrounging ('proportion scrounged', see *Definitions* below) covary with the speed of
117 production learning? 3. Is there repeatable individual variation in proportion scrounged? 4. Are the
118 variance components, and, hence, repeatability of production learning speed confounded by proportion
119 scrounged? 5. Is the covariance between these two traits primarily driven by within- or among-individual
120 variation? We discuss how our results offer insight into how cognition may influence the use of
121 alternative tactics to determine individual variation in foraging behaviours in complex social
122 environments.
123
124 METHODS
125
126 *General study design and measurement of production learning*
127
128 The dataset includes measures of scrounging behaviour from winter 2017-2018 in a population of great
129 tits and blue tits as they participated in a series of associative learning experiments (Reichert et al., 2020),
130 set within a long-term field study in Wytham Woods, Oxfordshire, UK (Perrins, 1965). A detailed

description of the design of the learning experiment is given elsewhere (Reichert et al., 2020). Briefly, individual birds in the population were given a leg ring with a passive integrative transponder (PIT tag; IB Technology, Aylesbury, UK), allowing for the identification of individuals that visited sunflower-seed feeders with a RFID antenna embedded within the perch below the single feeder opening. At least 90% of the population was estimated to be tagged (Aplin et al., 2013). A linear array of five feeders, spaced 1 m apart, was placed in each of four locations in 2017 and a different set of four locations in 2018. Arrays were placed to minimize overlap between groups of individuals, which typically forage in specific areas of the woodland; rare visits by individuals to feeders in arrays other than the one to which they were assigned were excluded (Reichert et al., 2020). After an initial acclimation period in which feeders were open to all birds, access to the feeders was regulated by a solenoid that held in place a transparent plastic door at the feeder opening. The feeders were programmed (via a printed circuit board; 'Darwin Board', Stickman Technologies Inc., UK) so that the solenoid released and allowed access to food only upon detection of specific PIT tags of birds assigned to that feeder (Firth & Sheldon, 2015). Each feeder was surrounded by a wire-mesh cage, which permitted birds to enter but prevented squirrels from damaging the feeder.

Individual birds were assigned randomly to be able to access just one of the five feeders in the array. Production learning therefore required that an individual visit its one assigned feeder and cease visiting the other four non-assigned feeders in the array (all feeders recorded all visits by all tagged birds, even if they were not rewarded). From the pattern of visits, we determined each individual's learning speed as the number of visits until it first met the criterion of visiting the correct feeder 80% of the time on 20 consecutive visits (in line with previous work (Reichert et al., 2020); there was no time limit for a visit to be considered consecutive), with the requirement that the first visit in that window be a correct visit. We performed three consecutive associative learning experiments: an initial learning experiment (eight days) followed by two consecutive reversals (eight days per reversal in 2017; and for operational reasons, ten days per reversal in 2018; see (Reichert et al., 2020)). In the reversal experiment, each bird was assigned

to a new feeder using one of two assignment methods. In four of the eight sites, each individual was reassigned to a randomly selected new feeder. In the other four sites, the entire group of birds originally assigned to each feeder was randomly reassigned to the same new feeder (e.g., all birds assigned to feeder 1 initially were reassigned to feeder 4 in the first reversal; all those assigned to feeder 2 were reassigned to feeder 1, etc.). The purpose of these treatments was to manipulate the social environment and partly control for social learning by manipulating the cohort of individuals assigned to the same rewarding feeder. Previous work on this dataset showed no influence of this treatment on production learning (Reichert et al., 2020). Note that we use the term 'production learning' to encompass behaviour in both initial and reversal learning experiments; separate production learning speeds were calculated for each experiment. Note also that although it is more typical for tests of reversal learning to alternate between only two options (Jentsch & Taylor, 2001; Laughlin, Grant, Williams, & Jentsch, 2011), reversal learning paradigms can involve more than two choices (Izquierdo, Brigman, Radke, Rudebeck, & Holmes, 2017). Because of this, and for consistency with similar studies (Reichert et al., 2020; Sonnenberg et al., 2019), we use the term reversal learning to describe our experiment.

Definitions

When individuals visited their assigned feeder, we defined them as playing the *producer* tactic. When the assigned bird left, there was a one second period before the door closed, potentially allowing an individual not assigned to that feeder to scrounge if it visited quickly enough (Supplementary Video 1). During such visits the solenoid did not release as normal, and therefore the food inside the feeder continued to be accessible as long as the individual remained on the perch (we note that the feeder opening was only large enough to allow one bird access at a time, and that after the individual left the solenoid did block access to the door again). We defined a *scrounge* as a visit by an unassigned bird taking place in this time interval (approximately one second; note that the timestamp recorded in the data file had a resolution of one second). Scrounges could be detected from the pattern of visits recorded on

183 the data file because the preceding individual was not recorded categorically as having "departed" if
184 another unassigned individual was detected accessing the perch before the door closed. This is because
185 the detection cycle of the antenna was too slow to register the departure of the preceding individual and
186 instead just reported the arrival of the new individual. Analysis of video footage confirmed that in these
187 cases individuals could and did access food (see Supplementary Material), and this was the only way
188 individuals could access food aside from producing. Tits generally take food items requiring processing,
189 such as sunflower seeds, away from the feeder into cover before eating; (Cole & Quinn, 2012; Hogstad,
190 1988), and we never observed any food left behind on the platform in the video analysis.
191
192 Both scrounges and produces were considered *rewarded visits* because they gave access to the sunflower
193 seeds inside of the feeder. Scrounges and produces were mutually exclusive strategies during any given
194 visit, when an individual could only act as a scrounger or a producer, satisfying one of the main
195 assumptions of producer-scrounger games (Giraldeau & Caraco, 2000). Producer-scrounger strategies are
196 quantified using the proportion of an individual's feeds that come from scrounging. Therefore, we define
197 an individual's *proportion scrounged* as the number times it scrounged divided by its total number of
198 rewarded visits (produces plus scrounges).
199
200 The aim of the analyses of learning to scrounge was to determine whether birds improved their ability to
201 scrounge with experience. Because of the tight time window for a bird to actually be able to access food
202 by scrounging, some attempts to scrounge must have failed. Evidence for learning to scrounge would be if
203 fewer such attempts failed with increasing visits. We define an *opportunity to scrounge* as taking place
204 when a bird made a visit to an unassigned feeder 5 s or less after the most recent previous visitor, which
205 had made a rewarded visit. If the arrival time was fast enough (< 1 s), then the bird could successfully
206 scrounge (see above); if the arrival was more than 1 s after the previous visitor, then the bird could not
207 obtain food by scrounging (Supplementary Video 2). The 5 s threshold is useful for understanding
208 learning to scrounge for two reasons: 1) It is possible that some such visits were not attempts by the bird

to scrounge, but instead were simply errors made by the bird attempting to find its own rewarding feeder, that just happened to occur shortly after another bird had fed at that feeder. It is not possible to cleanly define a time threshold separating these two possibilities. However, even if the bird were not attempting to scrounge, it is likely that in the process of visiting an otherwise unrewarding feeder shortly after a previous bird's visit, the subject bird had an opportunity to make an association between the speed of its arrival to such feeders and the availability of reward. In other words, these are opportunities to scrounge. 2) Our results, particularly those examining proportion scrounged across all of the experiments, were generally robust to several different choices of interval (Table S1), suggesting that despite any noise added by including some visits where the bird was simply choosing the wrong feeder, there is a strong pattern in the change in the ability to scrounge over time.

Data analysis

Most of our analyses focus on relationships between production learning and scrounging; therefore analyses were restricted to the set of 221 individuals that met the learning criterion in the initial learning experiment, and to the 198 and 183 individuals, respectively, that continued to meet the criteria in the subsequent two reversal learning experiments. Analyses that included data from all three experiments were done on the N=183 individuals that met the criterion in every experiment. Most individuals that did not meet the learning criterion for any given experiment did so not because they were making large numbers of scrounging visits but because they failed to participate in the experiment at all, making fewer than 50 visits to the feeders (Reichert et al., 2020). We measured all scrounges performed by an individual, including scrounges on heterospecific individuals, and also scrounges an individual made on birds that were otherwise excluded from the analyses because they did not meet the learning criterion. We note that individuals varied in the number of rewarded visits made (minimum = 21, maximum = 785), which may affect the precision of estimates of proportion scrounged.

Using this data set, we addressed five main questions arising from this experiment:

1. Did individuals learn to scrounge more efficiently? Evidence for learning to scrounge more efficiently would be if individuals had a higher proportion of scrounges with increasing opportunities to scrounge, and if the interval between the previous bird's departure and an individual's arrival at the feeder decreased with increasing opportunities to scrounge. However, because not all individuals visited an equal number of times, a similar pattern could arise via selective disappearance in which individuals that are initially largely unsuccessful at scrounging make very few attempts to do so, while individuals that are initially successful continue to make many scrounging visits. To differentiate between these possibilities, we used within-subject centring (van de Pol & Wright, 2009) in which we partitioned the fixed effect (visit number) into two components, calculated separately for each individual: its average visit number, representing the between-subjects effects and corresponding to any effect of selective disappearance, and the difference between each visit number and the average, representing the within-subject effects and corresponding to evidence for improved scrounging efficiency via learning. We used generalized linear mixed models (GLMMs) with the above fixed effects along with a fixed effect of experiment (initial, first reversal, second reversal), individual identity as a random effect, and as the dependent variable either the outcome of the visit (successful or unsuccessful scrounge, as defined above; binomial distribution) or the interval between an individual's arrival and the previous bird's departure for all scrounging opportunities (Poisson distribution, with an additional observation level random effect to control for overdispersion). When a successful scrounge took place, by definition the departure time of the first bird was unknown (see Definitions, above). Because scrounging was only possible within one second of the previous feed, we assigned a value of one second to the interval for these cases, unless the interval between the arrival of the first bird and the arrival of the second bird was recorded as zero (which happened if two birds arrived in very short succession at the perch; note that the order of visits was still recorded correctly in these cases).

These models were run for the combined set of visits across all three experiments. Models were run using the lme4 1.1-23 package (Bates, Maechler, Bolker, & Walker, 2015) in R 4.0.2 software (R Development Core Team, 2021). We confirmed that all GLMMs met model assumptions using residual diagnostic plots in the DHARMa package in R (Hartig, 2020).

2. Is proportion scrounged related to the speed of production learning? We used a mixed model in which production learning speed (ln-transformed) was the dependent variable (Gaussian), and individual identity was a random effect (a model with identity nested within site was singular, so site was excluded). We included as fixed effects experiment (initial, first reversal, second reversal), proportion scrounged, and the interaction between experiment and proportion scrounged (to determine if any covariation between scrounging and production learning speed varied across the experiments). Proportion scrounged was arcsine square root transformed. We also included the following fixed effects to control for variables that were identified in a previous study (Reichert et al., 2020) as being related to production learning speed in some or all of the three experiments: species, whether or not the feeder was located on the edge of the array (generally, birds assigned to edge feeders learned faster), the amount of time in hours in which the individual's assigned, and non-assigned, feeders were not operating because of a malfunction (birds that learned slower experienced longer durations). The latter variable may add some noise to the estimate of production learning but we do not expect it to affect scrounging because the result was that producers could not access the feeders as normal, so there was no opportunity to scrounge (i.e., no inconsistency in the reward schedule).

3. Is scrounging behaviour repeatable? For the purposes of these analysis, we calculated proportion scrounged on each day of an experiment for each individual. We calculated repeatability values by dividing the variance in proportion scrounged associated with individual identity by the sum of that variance, the residual variance, and the distribution-specific variance on the link scale following (Nakagawa, Johnson, & Schielzeth, 2017), using variance components calculated with Bayesian Markov-

chain Monte Carlo (MCMC) models in the MCMCglmm version 2.29 package (Hadfield, 2010) in R. We modelled proportion scrounged as a binomial dependent variable. Day number of the experiment was a fixed factor, individual identity was a random factor, and we used an inverse gamma prior (V=1, nu=1.002) (Dingemanse & Dochtermann, 2013). We ran 1.3 million iterations with a burn-in of 30,000 and a thinning interval of 1000 (effective sample size = 1270). We calculated the posterior mode and 95% highest posterior density (HPD) intervals of repeatability estimates. Separate values were calculated for each species in each experiment. We also calculated the repeatability of the overall proportion scrounged across the three experiments, with experiment as a fixed factor.

4. How does scrounging affect the repeatability of reversal learning speed? Separate mixed-model analyses were performed for each species. We did not include initial learning speed because although reversal learning speed was found to be significantly repeatable in previous analyses that did not account for scrounging (Reichert et al., 2020), there was no significant repeatability in learning speed across all three experiments (i.e., including initial learning speed in addition to the reversals). Reversal learning speed (ln-transformed) was the dependent variable, individual identity was the random effect, and experiment was an additional fixed effect along with feeder location and the malfunctioning times of the feeders as described above. We compared models with and without an additional fixed effect, proportion scrounged (arcsine square root transformed), to determine to what extent scrounging influenced within- versus among-individual variance components for reversal learning speed. We did this by extracting these variance components for the model that included proportion scrounged as a fixed effect, and compared them to the variance components calculated from a model that did not include proportion scrounged. We then calculated repeatabilities of reversal learning speed with and without accounting for proportion scrounged using the rptR 0.9.22 package (Stoffel, Nakagawa, & Schielzeth, 2017) in R. We used the rptR method here to match our previous analyses of the repeatability of production learning (Reichert et al., 2020) (similar results were obtained when using MCMC, see Table S2); we used the MCMC method

312 above because in those analyses the rptR method sometimes gave unreliable estimates because of
313 singularity issues.
314
315 5. Does the covariance between proportion scrounged and production learning (see Results) arise
316 primarily due to within-individual correlations, or consistent differences among individuals in these
317 behaviours? We ran MCMC models as above, with proportion scrounged (binomial) and production
318 learning speed (ln; Gaussian distribution) as dependent variables, a separate intercept fitted for each
319 dependent variable, individual identity as a random effect, and experiment as a fixed effect (data from all
320 three experiments were included). Separate models were run for each species because we were interested
321 in among-individual covariance as an indication of the potential for genetic covariance and a correlated
322 response of these traits to selection. We extracted within- and among-individual covariance components
323 by calculating the posterior mode and 95% HPD intervals of these elements from a variance-covariance
324 matrix (specified as unstructured). All MCMC models reported in this paper had autocorrelation less than
325 0.01.

RESULTS

Learning to scrounge

Scrounging was an alternative tactic to producing, and was not simply a by-product of individuals unable to access their own feeder due to other birds being present at the same feeder: 82.3% of all scrounges took place when no other bird had visited the scrounging individual's assigned feeder in the 10 s before the scrounge. The interval between one bird's arrival and the previous bird's departure differed between visits to the assigned feeder, and visits to non-assigned feeders, with only the latter revealing a large peak at the short time interval required for scrounging (Fig. S1). This indicates a clear signature of scrounging in this automated dataset.

Scrounging success increased with the number of scrounging opportunities (Fig. 1A). There was a significant between-subjects effect of average visit number on scrounging success (Table 1), indicating that some of the pattern of improved scrounging efficiency in Fig. 1A is due to individuals with low initial success at scrounging dropping out of the dataset after few visits (i.e., selective disappearance). However, there was also a significant within-subjects effect of visit number, which is evidence that the likelihood of success increased with increased visits, supporting the hypothesis that individuals learned to scrounge more efficiently. Correspondingly, there was a significant negative relationship between the time interval between a previous bird's successful production and an individual's own arrival at a non-assigned feeder and both the between- and within-subject components of visit number (Table 2; Fig. 1B). The latter result indicates evidence for improved scrounging efficiency even after controlling for selective disappearance, consistent with the hypothesis that scrounging efficiency is improved by learning. For both measures, the improvement in scrounging success levelled off by around 200 visits, suggesting a limit on scrounging success (Fig. 1).

352 Table 1. Evidence for learning to scrounge

353

Dependent variable	*N*	Effect	Estimate	SE	z	P
Scrounge–yes/no	183	Intercept	-1.062	0.072	-14.74	<0.001
		Visit number − average	0.001	0.0003	4.17	<0.001
		Average visit number	0.006	0.001	8.32	<0.001
		Experiment (first reversal)	0.17	0.04	3.80	<0.001
		Experiment (second reversal)	0.21	0.06	3.58	<0.001
Interval	183	Intercept	0.693	0.023	29.72	<0.0001
		Visit number − average	-0.001	0.0001	-5.90	<0.001
		Average visit number	-0.002	0.0002	-8.88	<0.001
		Experiment (first reversal)	-0.028	0.017	-1.65	0.10
		Experiment (second reversal)	-0.079	0.021	-3.74	<0.001

354

355 GLMM output with fixed factors generated by within-subjects centring (see *Methods*). Visit number –
356 average represents the within-subject effects and corresponds to evidence for learning to scrounge more
357 efficiently across visits. Average visit number represents the between-subjects effects and corresponds to
358 selective disappearance (i.e., fewer total visits) of less efficient scroungers. The measure of scrounging
359 success was the dependent variable: either whether the bird successfully scrounged on that visit, or the
360 interval between an individual's arrival on the feeder and the previously rewarded individual's departure
361 (up to a maximum of 5 s). Experiment was an additional fixed factor (reference level = initial).

362 *Production learning versus scrounging*

363

364 Individuals that were slower to learn the location of their assigned feeder exhibited a higher proportion
365 scrounged (estimate±SE: 2.89±0.52, t=5.55, P<0.001; Fig. 2). There was no significant interaction
366 between the experiment and proportion scrounged on learning speed (scrounging × first reversal:
367 estimate: −0.52±0.75, t=−0.70, P=0.49; scrounging × second reversal: estimate: -0.11±0.71, t=-0.15,
368 P=0.88; full model results in Table S3). Individuals whose very first experience of a reward was by
369 scrounging, rather than producing, learned more slowly (estimate: 0.61±0.11, t=5.71, P<0.001).

370

371 *Repeatability of scrounging*

372

373 Most individuals scrounged rarely, but there was substantial individual variation in proportion scrounged
374 (Fig. S3; e.g., 25/221 individuals scrounged on 10% or more of their rewarded visits during the initial
375 learning experiment). For both species, proportion scrounged was moderately repeatable across days
376 within each experiment (Table 2). However, overall proportion scrounged within an experiment was only
377 weakly repeatable across experiments (combined column, Table 2). Overall levels of scrounging
378 increased across the three experiments (median proportion scrounged for N=183 individuals that met the
379 production learning criterion in all experiments; initial learning: 0.92%; first reversal: 1.8%; second
380 reversal: 2.0%), and were significantly higher in both reversal learning experiments compared to the
381 initial learning experiment (GLMM with proportion scrounged as dependent variable (binomial),
382 experiment as fixed factor, an observation-level random effect and individual identity nested within site
383 as a random effect; first reversal: estimate=0.52±0.16, z=3.20 P=0.001; second reversal:
384 estimate=0.56±0.16, z=3.46 P<0.001).

385

386

Table 2. Repeatability of proportion scrounged

	Initial	First reversal	Second reversal	Combined
Great tit	0.389 (0.265,0.508)	0.346 (0.235,0.468)	0.312 (0.203,0.415)	0.066 (0.018,0.155)
Blue tit	0.474 (0.392,0.559)	0.205 (0.165,0.291)	0.369 (0.300,0.457)	0.065 (0.023,0.168)

Repeatability estimates are posterior modes (95% HPD interval) of the ratio of the variance explained by individual identity to the sum of that variance, the residual variance and the distribution-specific variance estimated from MCMC models. Values for the initial, first and second reversals are estimates of the repeatability of proportion scrounged by day within an experiment. The Combined column is the estimate of repeatability of proportion scrounged across the three experiments.

Effects of scrounging on repeatability of production learning

The repeatability estimate for production learning speed was significant or trended towards significance for both species (Table 3). However, the estimate for the repeatability of production learning speed was reduced, especially for the great tit, and not significant for either species when proportion scrounged was added to the model as a fixed effect, although there was wide overlap in the confidence intervals of all models (Table 3). The models of production learning speed including proportion scrounged provided better fits to the data than models without scrounging (great tits: Wald test, χ_1^2=34.0, P<0.001; blue tits: χ_1^2=24.5, P<0.001). Including proportion scrounged reduced within- and among-individual variance by a similar amount in blue tits; in great tits there was a larger decrease in the among-individual variance (Table 3).

Covariance between scrounging and production learning

The covariance between production learning speed and proportion scrounged was almost entirely explained by within-individual covariance for great tits (Table 4). The among-individual component was very small, with HPD intervals that crossed zero. In contrast, for blue tits, although within-individual covariance was again the larger component, it explained only 70.8% of the total covariance (Table 4). The among-individual component explained 29.2% of the covariance, and the HPD intervals did not cross zero, suggesting that the covariance between proportion scrounged and production learning speed was non-zero both within and among individual blue tits.

418 Table 3. Estimates of repeatability of reversal learning speed and variance components either including or
419 not including proportion scrounged in the statistical model

		r	95% CI	P	V_{within}	V_{Among}
Great tit	Scrounging not included	0.275	0.062, 0.502	0.010	1.31 (0.22)	0.50 (0.24)
	Scrounging included	0.147	0, 0.399	0.113	1.18 (0.20)	0.20 (0.16)
Blue tit	Scrounging not included	0.132	0, 0.324	0.078	1.08 (0.14)	0.16 (0.12)
	Scrounging included	0.097	0, 0.295	0.150	1.00 (0.13)	0.11 (0.10)

420

421 Repeatability estimates (r; 95% confidence interval, P-value) from mixed model analyses. V_{within} and
422 V_{Among} give the within- and among-individual variance (SE), respectively, estimated from linear mixed
423 models. *N*=68 great tits, 115 blue tits.

424

425

Table 4. Variance-covariance matrices for among- and within-individual covariation in proportion scrounged and number of visits to reach the production learning criterion

Great tit		Proportion scrounged	Number visits to learn
Among individual	Proportion scrounged	**0.475 (0.135, 1.144)**	0.321 (-0.435, 0.669)
	Number visits to learn	0.003 (-0.156, 0.294)	**0.180 (0.073, 0.392)**
Within individual	Proportion scrounged	**3.181 (2.249, 4.008)**	0.642 (0.531, 0.735)
	Number visits to learn	1.444 (1.088, 2.026)	**1.984 (1.536, 2.357)**
Blue tit			
Among individual	Proportion scrounged	**1.454 (0.952, 2.215)**	0.563 (0.258, 0.824)
	Number visits to learn	0.334 (0.081, 0.597)	**0.196 (0.095, 0.359)**
Within individual	Proportion scrounged	**1.600 (1.296, 2.010)**	0.500 (0.368, 0.573)
	Number visits to learn	0.811 (0.573, 1.046)	**1.600 (1.380, 1.882)**

Estimates are posterior modes (95% HPD interval; see Figs. S4-S5 for posterior distributions of each component) for among-individual and within-individual components from multivariate MCMCglmms of covariance between proportion scrounged and production learning speed ("Number of visits to learn"; larger values equal slower learning) across the experiments for each species (*N*=68 great tits, 115 blue tits), using an inverse gamma prior (similar results were obtained using an inverse Wishart prior; see Table S4; Figs. S4-S5). Variances are in bold along the diagonal, covariances on the bottom left, and the corresponding correlation is on the top right of each 2 x 2 matrix.

DISCUSSION

Using a large-scale experiment, we showed that scrounging success improved with number of attempts, suggesting that individuals learned to scrounge more efficiently. Individuals that were slower at learning to produce scrounged more often. Although overall levels of scrounging were low, the proportion of feeds that were scrounges ('proportion scrounged') was significantly and moderately repeatable across days within each experiment. The repeatability of learning speed was reduced substantially after controlling for proportion scrounged. Finally, we found that the covariance between production learning speed and proportion scrounged is driven by within-individual variation in the use of each tactic and, for blue tits, also by consistent among-individual differences.

Learning to scrounge

One of our key findings was that individuals learned to improve their success at scrounging by arriving to feeders more rapidly after a previous producer's visit, so as to be able to exploit the food access that the producer facilitated. This is a rare empirical demonstration in wild animals that individuals can learn to improve their efficiency at scrounging, and to our knowledge, the only demonstration of learning to produce and learning to scrounge in the same system. Although not discussed in the context of cognition, results presented in a previous study of this population also suggest that great tits learn to scrounge, in this case in the context of individuals following social partners who are able to access food (Firth et al., 2015). Many cognitive studies focus exclusively on production learning, but if scrounging during the experiment is possible, and if it is learned, then it will be important to look at the dynamics of learning of each behaviour to understand the role of cognition on foraging. In general, multiple behaviours, each with a cognitive component, may interact with one another to determine performance, raising the question of how these covary, and how to isolate specific cognitive mechanisms in experiments aiming to compare

performance across individuals (Griffin, Healy, & Guillette, 2015; Shaw & Schmelz, 2017; van Horik, Langley, Whiteside, & Madden, 2019).

We can rule out alternative explanations for the improvement in scrounging success over time. For instance, birds could become bolder with experience at the feeder, causing them to arrive sooner after a previous bird's visit. If so, then we would also expect to see decreasing intervals between an individual's arrival and the previous bird's departure across production visits, but instead there was no such change in interval across these visits (Fig. S6). Another possibility is that an individual's visits following another bird are attempts at social learning. We designed this experiment to reduce social learning in production as much as possible by assigning different individuals to different feeders (Reichert et al., 2020), though birds may still be attracted to an unassigned feeder through local enhancement. This is not incompatible with our interpretation of scrounging, however, and such local enhancement effects may instigate making the association between arriving quickly after another bird and reward, which ultimately leads to learning to scrounge effectively (Arbilly & Laland, 2014; Heyes, 1994). Finally, a pattern like that shown in Figure 1 could arise solely due to selective disappearance, if individuals that are poor scroungers also make few attempts. Indeed, there was evidence that individuals that scrounged more efficiently made more visits with the opportunity to scrounge. However, we also found evidence for within-subject effects of visit number, which indicates that even after accounting for selective disappearance effects, there was a general improvement in scrounging with increasing visits, which is evidence that learning was responsible for improved scrounging efficiency in this system.

Cognition, variation, and foraging tactics

Theory suggests that individual variation in performance on cognitive mechanisms required for producing may be influenced by the expression of alternative tactics such as scrounging (Beauchamp, 2000), and indeed, we found that individuals that scrounged more were also slower to learn the association with their

488 rewarded feeder in the production task. Accounting for proportion scrounged reduced the estimate of the
489 repeatability of learning speed in the reversal learning experiments. Although the reduction itself was not
490 significant, it did affect the statistical significance of the repeatability estimate. There is a strong interest
491 in estimating repeatability of cognitive traits to give insights into the stability of individual variation and
492 potential for natural selection on cognitive variation (Cauchoix et al., 2018; Morand-Ferron, Cole, &
493 Quinn, 2016), but our results indicate that alternative tactics are an important consideration because they
494 affect repeatability estimates.
495
496 While many studies have demonstrated a negative correlation between scrounging and production
497 learning (Aplin & Morand-Ferron, 2017; Fragaszy & Visalberghi, 1989; Lefebvre & Helder, 1997), ours
498 is the first to make repeated measurements of these behaviours in order to determine whether the
499 correlation between proportion scrounged and production learning speed arises primarily due to variation
500 within or among individuals. We found that the predominant covariance component was at the within-
501 individual level; the among-individual covariance component was much smaller, and essentially zero for
502 great tits. However, for blue tits, among-individual covariance was significantly greater than zero, which
503 indicates that some covariance between production learning speed and proportion scrounged was also
504 determined by consistent differences among individuals in the use of these two different foraging tactics.
505 Phenotypic covariance makes genetic covariance more likely, which if this were indeed the case, would
506 suggest the potential for a correlated response to selection acting on these alternative tactics or their
507 cognitive mechanisms (e.g., improved scrounging success could come at the cost of reduced production
508 learning ability) (Morand-Ferron et al., 2016). Nevertheless, the among-individual covariance could arise
509 from environmental effects that covary with individual behaviours (Morrissey, Kruuk, & Wilson, 2010).
510 Why there is among-individual covariance for one species and not the other could be due to an emergent
511 genotype × social-environment effect in a mixed species context, or because among-individual covariance
512 is present but masked by environmental covariance (Morrissey et al., 2010). Whatever the reason for the
513 difference, consistency is often exaggerated when measured over short time scales (Bell, Hankison, &

514 Laskowski, 2009), suggesting that within-individual variation, that is, individual behavioural plasticity,
515 was the main driver of the covariation between alternative tactics for both species, not intrinsic
516 differences between individuals.
517
518 Although individuals were highly plastic in their choice of tactic, absolute levels of scrounging were
519 relatively low. In socially foraging species, whether an individual adopts the producer or scrounger role
520 varies with the costs and benefits of each tactic (Giraldeau & Caraco, 2000). The low levels of scrounging
521 in our study were likely due to the relative ease of learning to produce food compared to acquiring it
522 through scrounging. Most individuals made the association with the rewarding feeder very quickly
523 (Reichert et al., 2020), and from then on could obtain food easily, as long as they continued to visit the
524 correct feeder. In contrast, scrounging required rapid and highly precise timing of visits after a previous
525 bird's rewarded visit (or, alternatively, that the scrounger actually chased the producer off the perch).
526 Thus, even though scrounging success greatly improved with experience (Fig. 1), individuals at most
527 scrounged successfully on about half of their opportunities. This high degree of difficulty means that the
528 net payoff for scrounging was likely quite low, and instead individuals put most of their effort into
529 producing, as predicted by theory (Giraldeau & Caraco, 2000). As our aim was to compare scrounging
530 levels and production learning speed, we did not analyse levels of scrounging for individuals that did not
531 meet the learning criterion. These individuals may have scrounged more often, although we note that very
532 few individuals that participated in the experiment failed to meet the learning criterion (Reichert et al.,
533 2020). In a previous study in the same population in which the production learning task was likely
534 substantially more challenging than ours, individual great tits were more likely to scrounge than they were
535 in the present study (Aplin & Morand-Ferron, 2017), which again matches theoretical predictions.
536
537 *Conclusions*
538

539 Our results serve as a reminder that individuals invariably have the choice to obtain food by doing
540 something other than participating in cognitive experiments in the wild. This may introduce biases in
541 measurements of cognitive performance, which have been addressed in past studies by quantifying or
542 controlling for participation rates (van Horik, Langley, Whiteside, & Madden, 2017), neophobia towards
543 novel experimental devices (Benson-Amram & Holekamp, 2012), motivation to obtain food (Diquelou,
544 Griffin, & Sol, 2016), and social learning (Reichert et al., 2020). Scrounging is rarely examined as a
545 potential confound, but in this study it was important in explaining variation in production learning speed.
546 In general, the realized performance of individuals on cognitive tests is a product of both their actual
547 cognitive capabilities and an array of factors not directly related to the targeted cognitive ability (Griffin
548 & Guez, 2014; Morand-Ferron et al., 2016; Rowe & Healy, 2014). Controlling for these confounding
549 effects, and for alternative foraging tactics, is a major but surmountable challenge for evolutionary
550 ecological studies of cognition in the wild.
551
552 Acquiring resources is undoubtedly cognitively challenging due to complex, heterogeneous social and
553 physical environments. Cognition has been suggested to improve our understanding of resource
554 acquisition in the context of contest behaviour (Reichert & Quinn, 2017); our results here suggest this is
555 also true for alternative foraging tactics in the producer-scrounger game. That alternative tactics can be
556 learned raises many possibilities for models and experiments on producer-scrounger games (see also
557 (Dubois, Morand-Ferron, & Giraldeau, 2010)). For example, how is the balance of producers and
558 scroungers in the population affected by improvement in individual performance of these tactics over
559 time, particularly if improvement in one tactic affects performance in the other? Is among-individual
560 covariance in tactic use driven by cognitive constraints, and how does this affect the outcome of
561 producer-scrounger games? What are the relative contributions of individual variation in cognitive ability
562 and heterogeneous individual experiences in a complex social environment in generating the high levels
563 of within-individual variation that we observed? Predictions from models incorporating learning of both

564 tactics could be tested in realistic social environments to investigate how individual performance and the
565 mix of cognitive abilities in the population interact to affect resource acquisition and fitness.

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567

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572

573 *Data accessibility*. Raw data are deposited in the Dryad Digital Repository
574 https://doi.org/10.5061/dryad.m0cfxpp43 (Reichert et al., 2021).

575

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FIGURE CAPTIONS

Figure 1. The relationship between visit number (only including visits in which there was an opportunity to scrounge, see *Definitions*) and **A** scrounging efficiency: the proportion of an individual's visits in each bin that were successful scrounges and **B**, the mean interval between a previous bird's rewarded visit and a potential scrounger's visit. The x-axis shows in chronological order the visit number in bins of 50 consecutive visits (i.e., the first bin corresponds to visits 1-50). Very few birds made more than 400 visits, so these visits (maximum=690) are combined into a single bin. Dots correspond to values for individual birds, and are jittered along the x-axis and rendered slightly transparent to reduce overlap. Horizontal bars represent mean (±SE) values across all birds within each bin. Note that in **B**, we plot the mean visit interval over 50 visits, which includes both scrounges (≤1 s) and visits in which there was an opportunity to scrounge but the bird did not successfully scrounge (>1 and <5 s). These values decrease over time but remain greater than 1 s because birds often did not arrive in time to scrounge (see **A**). *N*=183 individuals; data combined across the experiments. Patterns were similar when each species was plotted separately (Fig. S2).

Figure 2. Relationship between (arcsine square-root transformed) proportion scrounged and (ln) number of visits until learning criterion was met (higher values indicate slower learning) in **A** initial learning, **B** the first reversal, and **C** the second reversal. Dots show individual birds (*N*=221, 198, and 183 for **A**, **B**, and **C**, respectively). Points with a value of zero for proportion scrounged are partially transparent and slightly jittered along the x-axis; all other points are fully opaque and correspond to exact values. Line represents linear least-squares regression, shaded area corresponds to 95% confidence interval.