

Cognition and covariance in the producer-scrourer game

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Cognition and covariance in the producer-scrourer game

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ABSTRACT

1. The producer-scrouter game is a key element of foraging ecology in many systems. Producing and scrounging typically covary negatively, but partitioning these sources of 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-scrouter 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 task that required individuals to learn which feeder in an array provided a food reward. Individuals could not access food from other feeders unless they scrounged by visiting a feeder immediately after a previous visitor. Three learning experiments – initial and two reversal learning – enabled us to estimate repeatability and covariance of performance in each foraging tactic.

3. First, we examined whether individuals learned to improve their scrounging performance. Second, we quantified the repeatability of scrounging behaviour, and asked whether scrounging affected production learning performance among individuals. Third, we used multivariate analyses to partition within- and among-individual components of covariance between scrounging and production learning.

4. Individuals improved their scrounging success over time. Birds that scrounged more took longer to learn their own rewarding feeder. Although multivariate analyses showed that covariance between scrounging levels 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, suggesting a potential role for genetic covariance between these traits.

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. Our results point to the potential for correlational selection to act on alternative foraging tactics. They also point to the need to control for these tactics when quantifying individual cognition in the wild.

47 Key words: alternative tactics, field experiment, individual differences, learning, repeatability, social
48 foraging
49

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 correlated 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 producing 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, the role of cognition in determining scrounging performance has 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 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 effects are on the probability of scrounging, however to our knowledge there are no empirical studies demonstrating that learning is involved in improved efficiency of scrounging. 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 performance (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) controlled feeding stations to selectively manipulate which individuals could access food in order to

measure individuals' production learning speeds in an associative (discriminant) learning task (Reichert et al., 2020). Scrounging was possible in this experimental set-up if individuals visited one of their non-rewarding RFID-controlled feeders very quickly after another individual obtained a reward (Firth et al., 2015). Here, we examined producer-scrounging behaviour during a production learning experiment and two reversal production-learning experiments to address the following questions: 1. Do individuals become more successful in scrounging over time, suggesting that they learn to scrounge? 2. Do scrounging levels covary with the speed of production learning? 3. Is there repeatable individual variation in the propensity to scrounge? 4. Are the variance components, and, hence, repeatability of production learning confounded by scrounging? 5. Is the covariance between these two traits primarily driven by within- or among-individual variation? We discuss how our results offer insight into how cognition may influence the use of alternative tactics to determine individual variation in foraging behaviours in complex social environments.

METHODS

General study design and measurement of production learning

The dataset includes measures of scrounging behaviour from winter 2017-2018 in a population of great tits and blue tits as they participated in a series of associative learning experiments (Reichert et al., 2020), 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).

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 the data file because the preceding individual was not recorded categorically as having “departed” if another unassigned individual was detected accessing the perch before the door closed. This is because the detection cycle of the antenna was too slow to register the departure of the preceding individual and instead just reported the arrival of the new individual. Analysis of video footage confirmed that in these cases individuals could and did access food (see Supplementary Material), and this was the only way individuals could access food aside from producing. Tits generally take food items requiring processing, such as sunflower seeds, away from the feeder into cover before eating; (Cole & Quinn, 2012; Hogstad, 1988), and we never observed any food left behind on the platform in the video analysis.

180

181 Both scrounges and produces were considered *rewarded visits* because they gave access to the sunflower
182 seeds inside of the feeder. Scrounges and produces were mutually exclusive strategies during any given
183 visit, when an individual could only act as a scrounger or a producer, satisfying one of the main
184 assumptions of producer-scrounger games (Giraldeau & Caraco, 2000). Producer-scrounger strategies are
185 quantified using the proportion of an individual's feeds that come from scrounging. Therefore, we define
186 the *proportion scrounged* as the number of scrounges divided by the total number of rewarded visits
187 (produces plus scrounges).

188

189 The aim of the analyses of learning to scrounge was to determine whether birds improved their ability to
190 scrounge with experience. Because of the tight time window for a bird to actually be able to access food
191 by scrounging, some attempts to scrounge must have failed. Evidence for learning to scrounge would be if
192 fewer such attempts failed with increasing visits. We define an *opportunity to scrounge* as taking place
193 when a bird made a visit to an unassigned feeder 5 s or less after the most recent previous visitor, which
194 had made a rewarded visit. If the arrival time was fast enough (< 1 s), then the bird could successfully
195 scrounge (see above); if the arrival was more than 1 s after the previous visitor, then the bird could not
196 obtain food by scrounging (Supplementary Video 2). The 5 s threshold is useful for understanding
197 learning to scrounge for two reasons: 1) It is possible that some such visits were not attempts by the bird
198 to scrounge, but instead were simply errors made by the bird attempting to find its own rewarding feeder,
199 that just happened to occur shortly after another bird had fed at that feeder. It is not possible to cleanly
200 define a time threshold separating these two possibilities. However, even if the bird were not attempting
201 to scrounge, it is likely that in the process of visiting an otherwise unrewarding feeder shortly after a
202 previous bird's visit, the subject bird had an opportunity to make an association between the speed of its
203 arrival to such feeders and the availability of reward. In other words, these are opportunities to scrounge.
204 2) Our results, particularly those examining scrounging performance across all of the experiments, were
205 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, 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. The sample sizes for these analyses were reduced (see Results) because not all birds made visits in which there was an opportunity to scrounge. 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, 2020). 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.

284

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

300

301 5. Does the covariance between proportion scrounged and production learning (see Results) arise
302 primarily due to within-individual correlations, or consistent differences among individuals in these
303 behaviours? We ran MCMC models as above, with proportion scrounged (binomial) and production
304 learning speed (ln; Gaussian distribution) as dependent variables, a separate intercept fitted for each
305 dependent variable, individual identity as a random effect, and experiment as a fixed effect (data from all
306 three experiments were included). Separate models were run for each species because we were interested
307 in among-individual covariance as an indication of the potential for correlational selection and genetic
308 covariance. We extracted within- and among-individual covariance components by calculating the

309 posterior mode and 95% HPD intervals of these elements from a variance-covariance matrix (specified as
310 unstructured). All MCMC models reported in this paper had autocorrelation less than 0.01.

RESULTS

Learning to scrounge

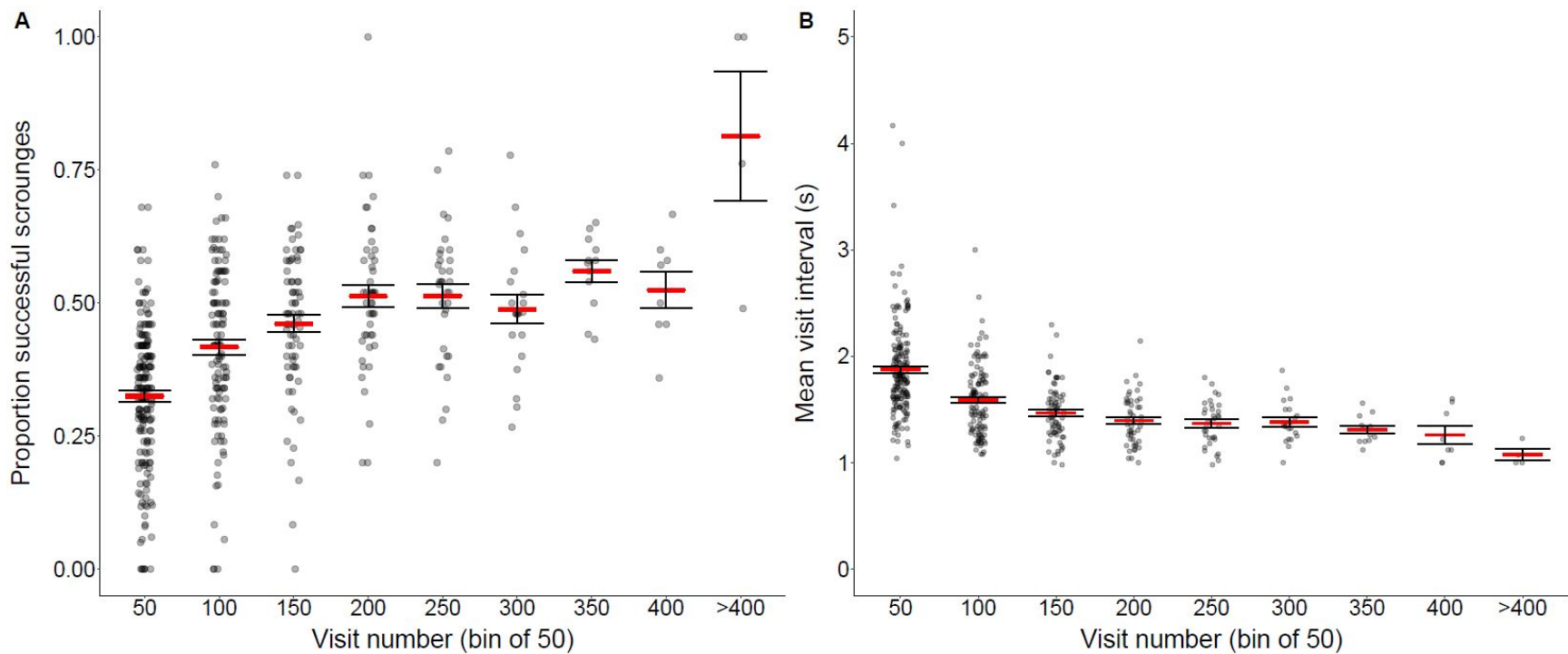
Scrounging was an alternative tactic to producing, and was not simply a by-product of individuals unable to access their own feeder due to other birds being present at the same feeder: 82.3% of all scrounges took place when no other bird had visited the scrounging individual's assigned feeder in the 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 performance 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 success improved 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 learned. For both measures, the improvement in scrounging success levelled off by around 200 visits, suggesting a limit on scrounging performance (Fig. 1).

Table 1. Evidence for learning to scrounge

Dependent variable	<i>N</i>	Effect	Estimate	SE	<i>z</i>	<i>P</i>
Scrounge–yes/no	183	Visit number – average	0.002	0.0002	8.90	<0.001
		Average visit number	0.006	0.001	8.32	<0.001
Interval	183	Visit number – average	-0.001	0.0001	-11.2	<0.001
		Average visit number	-0.002	0.0002	-9.05	<0.001

GLMM output with fixed factors generated by within-subjects centring (see *Methods*). Visit number – average represents the within-subject effects and corresponds to evidence for learning to scrounge more efficiently across visits. Average visit number represents the between-subjects effects and corresponds to selective disappearance (i.e., fewer total visits) of less efficient scroungers. The measure of scrounging success was the dependent variable: either whether the bird successfully scrounged on that visit, or the interval between an individual's arrival on the feeder and the previously rewarded individual's departure (up to a maximum of 5 s). Sample sizes are reduced because some birds never made visits in which there was an opportunity to scrounge.



348

349 Figure 1. The relationship between visit number (only including visits in which there was an opportunity to scrounge, see *Definitions*) and **A** the
350 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
351 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
352 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
353 correspond to values for individual birds, and are jittered along the x-axis and rendered slightly transparent to reduce overlap. Horizontal bars
354 represent mean (\pm SE) values across all birds within each bin. Note that in **B**, we plot the mean visit interval over 50 visits, which includes both
355 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

356 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
357 across the experiments. Patterns were similar when each species was plotted separately (Fig. S2).

Production learning versus scrounging

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

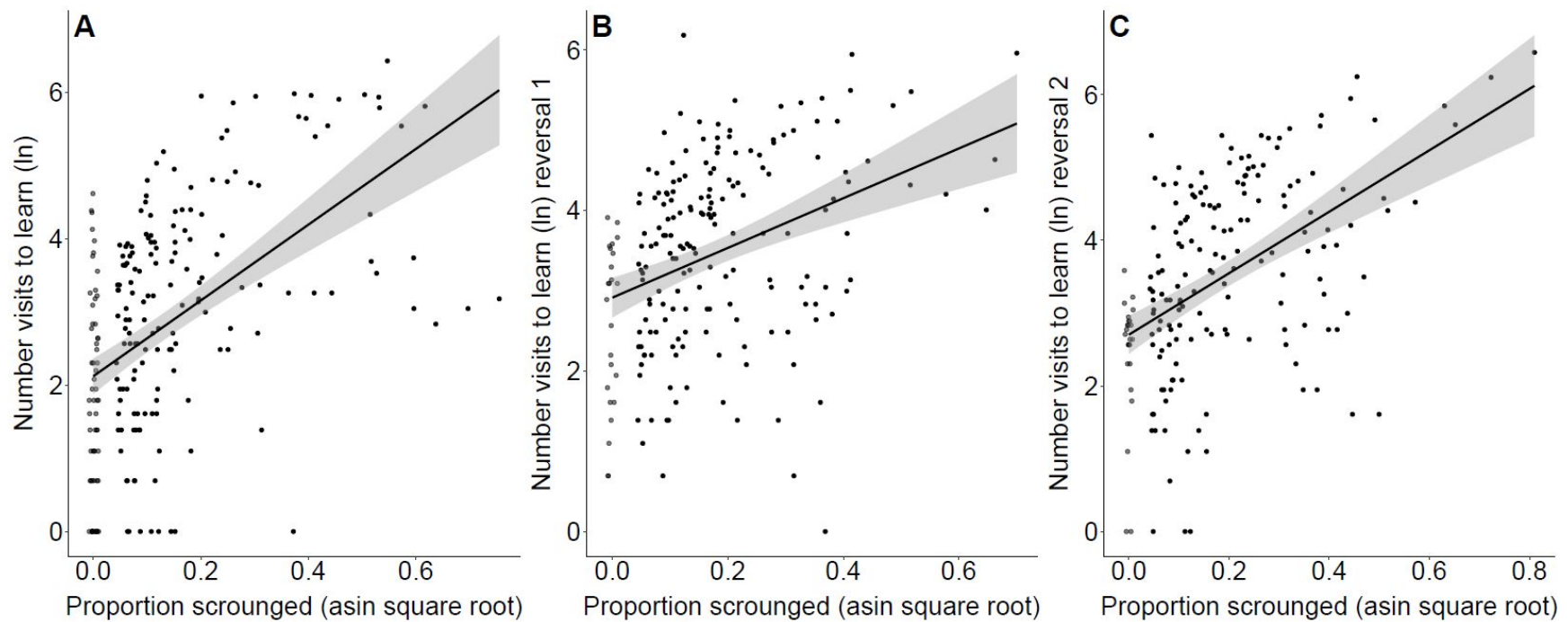


Figure 2. Relationship between (arcsine square-root transformed) proportion scrounged and (ln) number of visits until learning criterion was met (higher values indicate slower learning) in **A** initial learning, **B** the first reversal, and **C** the second reversal. Dots show individual birds ($N=221$, 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.

Repeatability of scrounging

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

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, $\chi^2=34.0$, $P<0.001$; blue tits: $\chi^2=24.1$, $P<0.001$). 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.

Table 3. Estimates of repeatability of reversal learning speed and variance components either including or 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	1.01 (0.13)	0.11 (0.10)

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

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 MCMCglms 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 increased with number of attempts, suggesting that individuals learned to scrounge. Individuals that were slower at learning to produce scrounged more often. Although overall levels of scrounging were low, scrounging proportion was significantly and moderately repeatable across days within each experiment. The repeatability of learning performance was reduced substantially after controlling for the effects of scrounging. 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 quicker after producers. 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, & Guillelte, 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 rewarded feeder in the production task. Accounting for scrounging reduced the estimate of the repeatability of performance in the reversal learning experiments. Although the reduction itself was not

significant, it did affect the statistical significance of the repeatability estimate. There is a strong interest in estimating repeatability of cognitive traits to give insights into the stability of individual variation and potential for natural selection on cognitive variation (Cauchoix et al., 2018; Morand-Ferron, Cole, & Quinn, 2016), but our results indicate that alternative tactics are an important consideration because they affect repeatability estimates.

While many studies have demonstrated a negative correlation between scrounging and production learning (Aplin & Morand-Ferron, 2017; Fragaszy & Visalberghi, 1989; Lefebvre & Helder, 1997), ours is the first to make repeated measurements of these behaviours in order to determine whether this correlation arises primarily due to variation within or among individuals. We found that the predominant covariance component was at the within-individual level; the among-individual covariance component was much smaller, and essentially zero for great tits. However, for blue tits, among-individual covariance was significantly greater than zero, which indicates that some covariance between production learning and proportion scrounged was also determined by consistent differences among individuals in the use of these two different foraging tactics. Phenotypic covariance makes genetic covariance more likely, which if this were indeed the case, would suggest the potential for antagonistic selection acting on these alternative tactics or their cognitive mechanisms (e.g., improved scrounging performance could come at the cost of reduced production learning ability) (Morand-Ferron et al., 2016). Nevertheless, the among-individual covariance could arise from environmental effects that covary with individual behaviours (Morrissey, Kruuk, & Wilson, 2010). Why there is among-individual covariance for one species and not the other could be due to an emergent genotype \times social-environment effect in a mixed species context, or because among-individual covariance is present but masked by environmental covariance (Morrissey et al., 2010). Whatever the reason for the difference, consistency is often exaggerated when measured over short time scales (Bell, Hankison, & Laskowski, 2009), suggesting that within-individual variation, that is, individual behavioural plasticity, was the main driver of the covariation between alternative tactics for both species, not intrinsic differences between individuals.

Although individuals were highly plastic in their choice of tactic, absolute levels of scrounging were relatively low. In socially foraging species, whether an individual adopts the producer or scrounger role varies with the costs and benefits of each tactic (Giraldeau & Caraco, 2000). The low levels of scrounging in our study were likely due to the relative difficulty of scrounging compared to producing. Most individuals made the association with the rewarding feeder very quickly (Reichert et al., 2020), and from then on could obtain food easily, as long as they continued to visit the correct feeder. In contrast, scrounging required rapid and highly precise timing of visits after a previous bird's rewarded visit (or, alternatively, that the scrounger actually chased the producer off the perch). Thus, even though scrounging success greatly improved with experience (Fig. 1), individuals at best scrounged successfully on about half of their opportunities. This high degree of difficulty means that the net payoff for scrounging was likely quite low, and instead individuals put most of their effort into producing, as predicted by theory (Giraldeau & Caraco, 2000). As our aim was to compare scrounging levels and production learning speed, we did not analyse levels of scrounging for individuals that did not meet the learning criterion. These individuals may have scrounged more often, although we note that very few individuals that participated in the experiment failed to meet the learning criterion (Reichert et al., 2020). In a previous study in the same population in which the production learning task was likely substantially more challenging than ours, individual great tits were more likely to scrounge than they were in the present study (Aplin & Morand-Ferron, 2017), which again matches theoretical predictions.

Conclusions

Our results serve as a reminder that individuals invariably have the choice to obtain food by doing something other than participating in cognitive experiments in the wild. This may introduce biases in measurements of cognitive performance, which have been addressed in past studies by quantifying or controlling for participation rates (van Horik, Langley, Whiteside, & Madden, 2017), neophobia towards

novel experimental devices (Benson-Amram & Holekamp, 2012), motivation to obtain food (Diquelou, Griffin, & Sol, 2016), and social learning (Reichert et al., 2020). Scrounging is rarely examined as a potential confound, but in this study it was important in explaining variation in production learning speed. In general, the realized performance of individuals on cognitive tests is a product of both their actual cognitive capabilities and an array of factors not directly related to the targeted cognitive ability (Griffin & Guez, 2014; Morand-Ferron et al., 2016; Rowe & Healy, 2014). Controlling for these confounding effects, and for alternative foraging tactics, is a major but surmountable challenge for evolutionary ecological studies of cognition in the wild.

Acquiring resources is undoubtedly cognitively challenging due to complex, heterogeneous social and physical environments. Cognition has been suggested to improve our understanding of resource acquisition in the context of contest behaviour (Reichert & Quinn, 2017); our results here suggest this is also true for alternative foraging tactics in the producer-scrounger game. That alternative tactics can be learned raises many possibilities for models and experiments on producer-scrounger games (see also (Dubois, Morand-Ferron, & Giraldeau, 2010)). For example, how is the balance of producers and scroungers in the population affected by improvement in individual performance of these tactics over time, particularly if improvement in one tactic affects performance in the other? Is among-individual covariance in tactic use driven by cognitive constraints, and how does this affect the outcome of producer-scrounger games? What are the relative contributions of individual variation in cognitive ability and heterogeneous individual experiences in a complex social environment in generating the high levels of within-individual variation that we observed? Predictions from models incorporating learning of both tactics could be tested in realistic social environments to investigate how individual performance and the mix of cognitive abilities in the population interact to affect resource acquisition and fitness.

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Data accessibility. Data will be deposited in the Dryad Digital Repository upon manuscript acceptance.

Authors' contributions. M.S.R., J.L.Q., J.A.F., G.L.D. and I.G.K. designed the experiment, M.S.R., G.L.D. and I.G.K. built experimental devices, M.S.R. and S.J.C. performed fieldwork, M.S.R., J.M.F., and J.L.Q. analysed data and M.S.R. wrote manuscript with input from all authors. All authors gave final approval for publication.

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Supplementary Methods and Results: Video Analyses

We analysed video recordings made during this experiment, and to bolster our sample size, recordings made using an identical setup in County Cork, Ireland. The aim of these analyses was to determine whether the visit record obtained from the RFID antenna corresponded to visual observations of each individual visit, and to determine whether visits we classified as scrounges in fact corresponded to an individual obtaining food by arriving quickly after another individual's rewarded visit. Videos covered 11 different feeders from 3 different sites, with a total of 280 minutes of footage.

We observed 699 visits (only those visits from RFID tagged birds are included; non-tagged birds occasionally landed on feeders but these could not access the feeders and are not of interest to this study). There were 57 scrounges. In each of these 57 scrounges the individual classified as a scrounger was able to access the seeds and took one. Therefore, we are confident that most, if not all, visits we classified as scrounges led to a food reward. We never observed an individual able to access food aside from either landing on its own rewarded feeder (i.e., producing) or scrounging, as defined in the Methods. Birds that accessed food generally took a single sunflower seed and flew away with it to process elsewhere, thus there was never any food left on the platform that may have acted as a reward to non-scrounging individuals.

Supplementary Video 1

A successful scrounge. In the video, a great tit is seen making a producing visit. After it departs a second great tit arrives and scrounges. Note that this video was taken from footage of visits in a population in County Cork, Ireland, that were not part of the present study, but using an identical feeder setup.

Supplementary Video 2

An unsuccessful attempt to scrounge. In this video, a great tit is seen making a producing visit. After it departs a blue tit arrives, but is slightly too late and so is unable to access the food. It pecks at the transparent door a few times but the door is blocked and it then flies off. This video was taken from footage of the present study, from Wytham Woods, Oxford, UK. Note the screen surrounding the feeder, this was to prevent squirrels and large birds like woodpeckers from damaging the feeders.

Table S1. Model results for learning to scrounge, using alternative maximum intervals (see ‘Interval threshold’ column) for when the potential scrounger arrived after the previous successful producer visit (i.e., for how we defined an opportunity to scrounge). We present results using the chosen interval threshold of 5 s in the text (Table 1). Alternatives of 2, 4 and 6 s are explored here. Analyses were generalized linear mixed models with the dependent variable of either whether the individual scrounged on the visit (binomial), or ‘Interval’: the amount of time between the individual’s arrival at the feeder and the time at which the previous, rewarded, bird had departed (see main text for further details). Fixed factors were generated by within-subjects centring (see *Methods*). Visit number – average represents the within-subject effects and corresponds to evidence for learning to scrounge more efficiently across visits. Average visit number represents the between-subjects effects and corresponds to selective disappearance (i.e., fewer total visits) of less efficient scroungers. Individual identity was the random effect. Sample sizes (*N*) vary because not all birds made visits in which they could have scrounged at some or all of these intervals.

Variable	Interval threshold	Effect	<i>N</i>	Estimate	SE	<i>z</i>	<i>P</i>
Scrounge – yes/no	2 s	Visit number – average	181	0.001	0.0002	4.41	<0.001
		Average visit number		0.005	0.0006	7.15	<0.001
	4 s	Visit number – average	183	0.002	0.0002	8.03	<0.001
		Average visit number		0.005	0.001	8.01	<0.01
	6 s	Visit number – average	183	0.002	0.0002	9.84	<0.001
		Average visit number		0.006	0.0007	8.41	<0.001
Interval	2 s	Visit number – average	181	-0.0002	0.0001	-1.93	0.053
		Average visit number		-0.0004	0.0001	-3.17	0.002
	4 s	Visit number – average	183	-0.0007	8.5E-5	-8.55	<0.001
		Average visit number		-0.002	0.0002	-8.44	<0.001
	6 s	Visit number – average	183	-0.0005	0.0002	-2.51	0.01
		Average visit number		-0.003	0.0005	-5.37	<0.001

Table S2. Estimates of the repeatability of scrounging, using the MCMCglmm method to calculate repeatabilities. In Table 3 in the main text we present repeatability values using the rptR function, to match with our previously published data. Here, we show estimates from an MCMC model calculated as in Table 2 (with the same fixed effects as those used to calculate repeatabilities in Table 3; see Methods). r is the estimate of repeatability, as the posterior mode of the ratio between the among and within individual variance components, along with the 95% HPD. V_w and V_{Among} give the posterior mode and HPD for the within- and among-individual variance, respectively (note that dividing the V_{Among} by the sum of V_w and V_{Among} that are presented in this table will not give the exact same value as the estimate of r , because we calculated r as the posterior mode of that ratio for each sample, and calculated separate posterior modes for V_w and V_{Among} . $N=68$ great tits, 115 blue tits.

		r	95% HPD	V_w (HPD)	V_{Among} (HPD)
Great tit	Scrounging not included	0.314	0.092, 0.458	1.29 (0.95,1.81)	0.51 (0.17,0.95)
	Scrounging included	0.192	0.074, 0.372	1.24 (0.81,1.50)	0.28 (0.10,0.58)
Blue tit	Scrounging not included	0.194	0.082, 0.331	1.01 (0.80,1.26)	0.21 (0.10,0.44)
	Scrounging included	0.169	0.072, 0.308	0.92 (0.72,1.16)	0.21 (0.08,0.38)

Table S3. Full model results for effects of scrounging and other variables on production learning speed. Learning speeds were natural log transformed. Proportion scrounged was arcsine square-root transformed. Estimates (calculated using restricted maximum likelihood), t values and P values are shown. The reference levels for categorical factors are as follows: species (blue tit), feeder location (centre), experiment (initial learning), first reward experience (producing). $N=183$ individuals. Learning speed is the number of visits to criterion, therefore positive effects represent slower learning. Individual identity was the random effect; a random effect of identity nested within site resulted in singularity issues, and so was excluded.

Fixed terms	Estimate	SE	t	P
Intercept	2.54	0.14	18.60	<0.001
Own feeder malfunctioning time (hrs)	0.06	0.01	4.50	<0.001
Other feeder malfunctioning time (hrs)	0.05	0.01	5.23	<0.001
Feeder location	-0.70	0.10	-7.20	<0.001
Species	-0.11	0.11	-1.07	0.28
Proportion scrounged	2.89	0.52	5.55	<0.001
Experiment (first reversal)	0.51	0.17	3.08	0.002
Experiment (second reversal)	0.32	0.16	1.95	0.052
First reward experience	0.61	0.11	5.71	<0.001
Proportion scrounged \times experiment (first reversal)	-0.52	0.75	-0.70	0.49
Proportion scrounged \times experiment (second reversal)	-0.11	0.71	-0.15	0.88

Table S4. Variance-covariance matrices for among and within individual covariation in proportion scrounged and learning speed, with an inverse Wishart prior.

Great tit		Proportion scrounged	Production learning speed
Among individual	Proportion scrounged	0.540 (0.202, 1.203)	0.066 (-0.324, 0.635)
	Production learning speed	0.010 (-0.136, 0.315)	0.230 (0.121, 0.503)
Within individual	Proportion scrounged	2.969 (2.204, 3.891)	0.654 (0.520, 0.726)
	Production learning speed	1.380 (1.090, 2.010)	1.924 (1.518, 2.355)
Blue tit			
Among individual	Proportion scrounged	1.568 (1.000, 2.146)	0.500 (0.232, 0.754)
	Production learning speed	0.318 (0.080, 0.578)	0.257 (0.144, 0.418)
Within individual	Proportion scrounged	1.624 (1.323, 2.036)	0.508 (0.386, 0.586)
	Production learning speed	0.799 (0.567, 1.040)	1.666 (1.376, 1.863)

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 MCMCglmm models of covariance between proportion scrounged and production learning speed across the experiments for each species ($N=68$ great tits, 115 blue tits), using an inverse wishart prior: `list(R=list(V=diag(2), nu=2),G=list(G1=list(V=diag(2), nu=2)))`. Results were similar to those calculated using an inverse gamma prior; see Table 4. In this case the among-individual component explained 28.5% of the covariance for blue tits (compared to 29.2% when calculated using inverse Gamma prior). Variances are on the diagonal, covariances on the bottom left, and the corresponding correlation on the top right of each matrix.

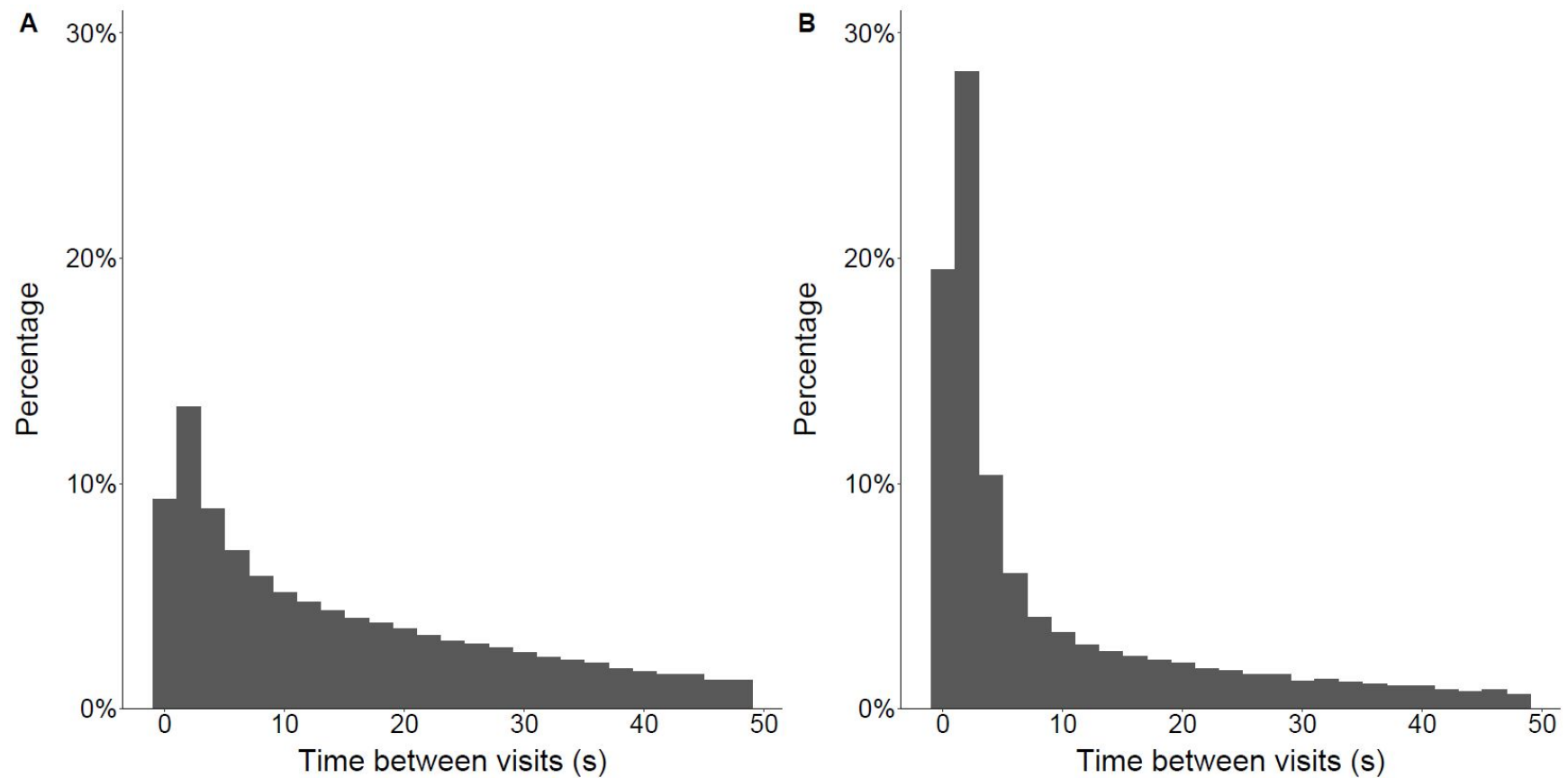


Figure S1: Histograms of the interval between visits (difference between the arrival time of the focal bird and the departure time of the previous bird) for **A** visits to the individual's assigned feeder (produces) and **B** visits to unassigned feeders (which includes both scrounge attempts, and errors during production learning). Only intervals of 50 s or less are shown. Histograms include data from all three experiments, only for those (N=183) birds that met the learning criterion in each experiment.

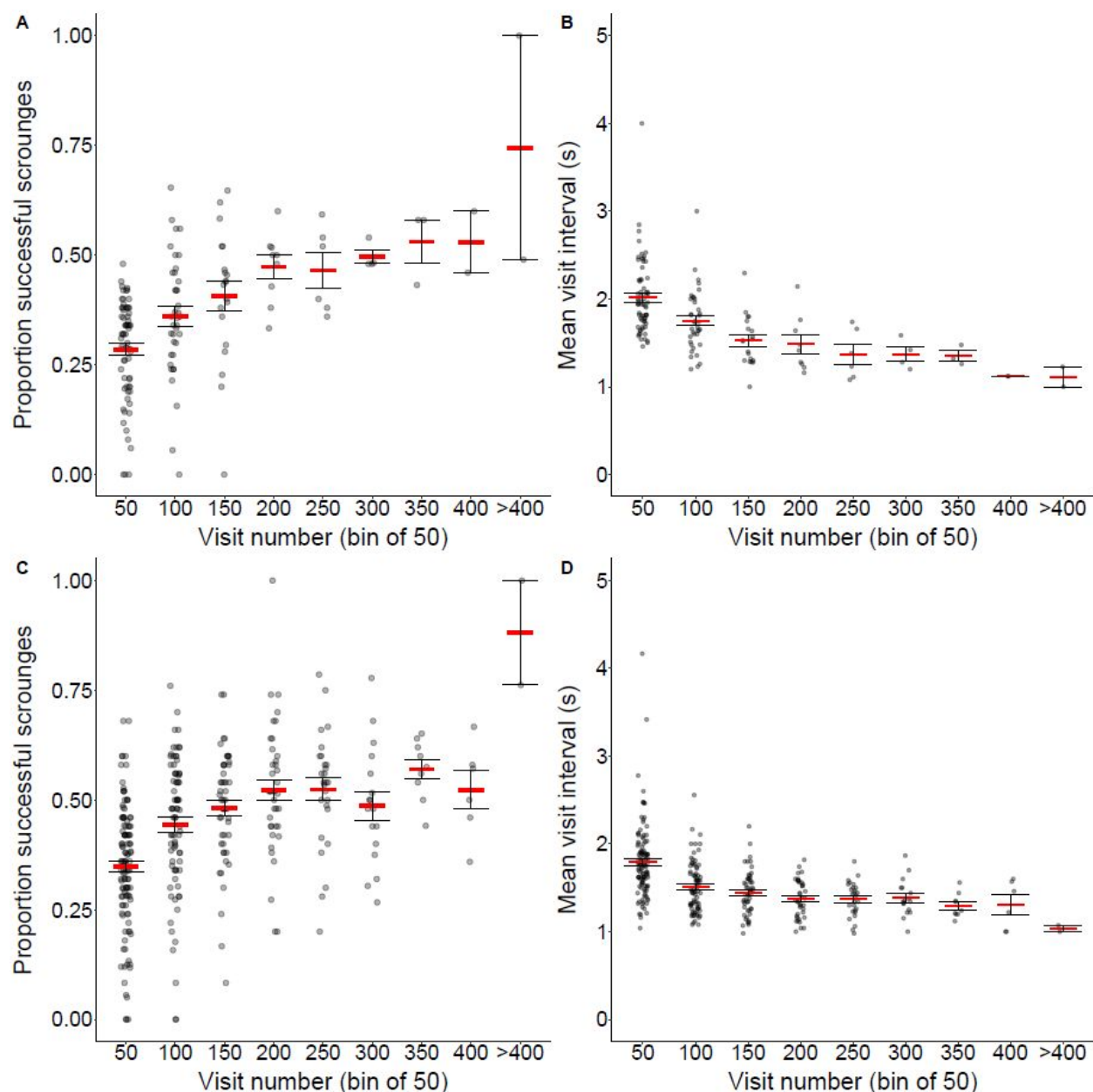


Figure S2. As in Figure 1 in the main text, but plotted separately for great tits (**A, B**) and blue tits (**C, D**). **A, C**: The relationship between visit number (only including visits in which there was an opportunity to scrounge, see *Definitions*) and the proportion of an individual's visits in each bin that were successful scrounges; **B, D**: The interval between a previous bird's rewarded visit and a potential scrounger's visit, combined across the three experiments. 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 (up to the maximum of 690) are combined into a single bin. The y-axis in **A, C** shows the proportion of visits in each bin that were successful, and **B, D** the mean interval between visits. Dots correspond to values for an individual bird, and have been jittered along the x-axis and rendered slightly transparent to reduce overlap. Horizontal bars represent mean values across all birds within each bin of visits. Error bars represent one standard error. Note that there are fewer samples at higher visit numbers because not all birds made that many visits. $N=68$ great tits, 115 blue tits.

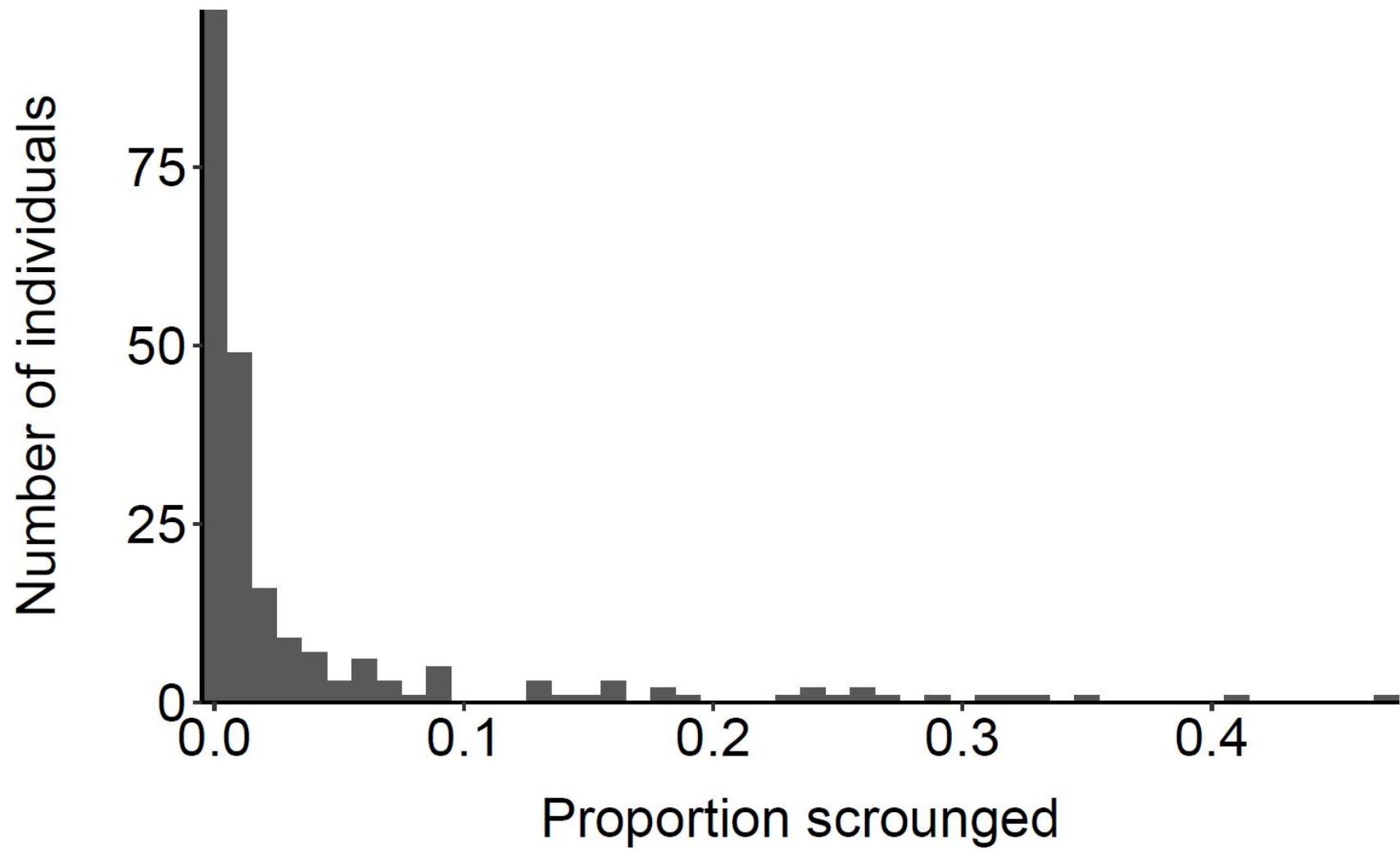


Figure S3. Histogram of proportion scrounged for individuals that met the learning criterion in the initial learning experiment ($N=221$)

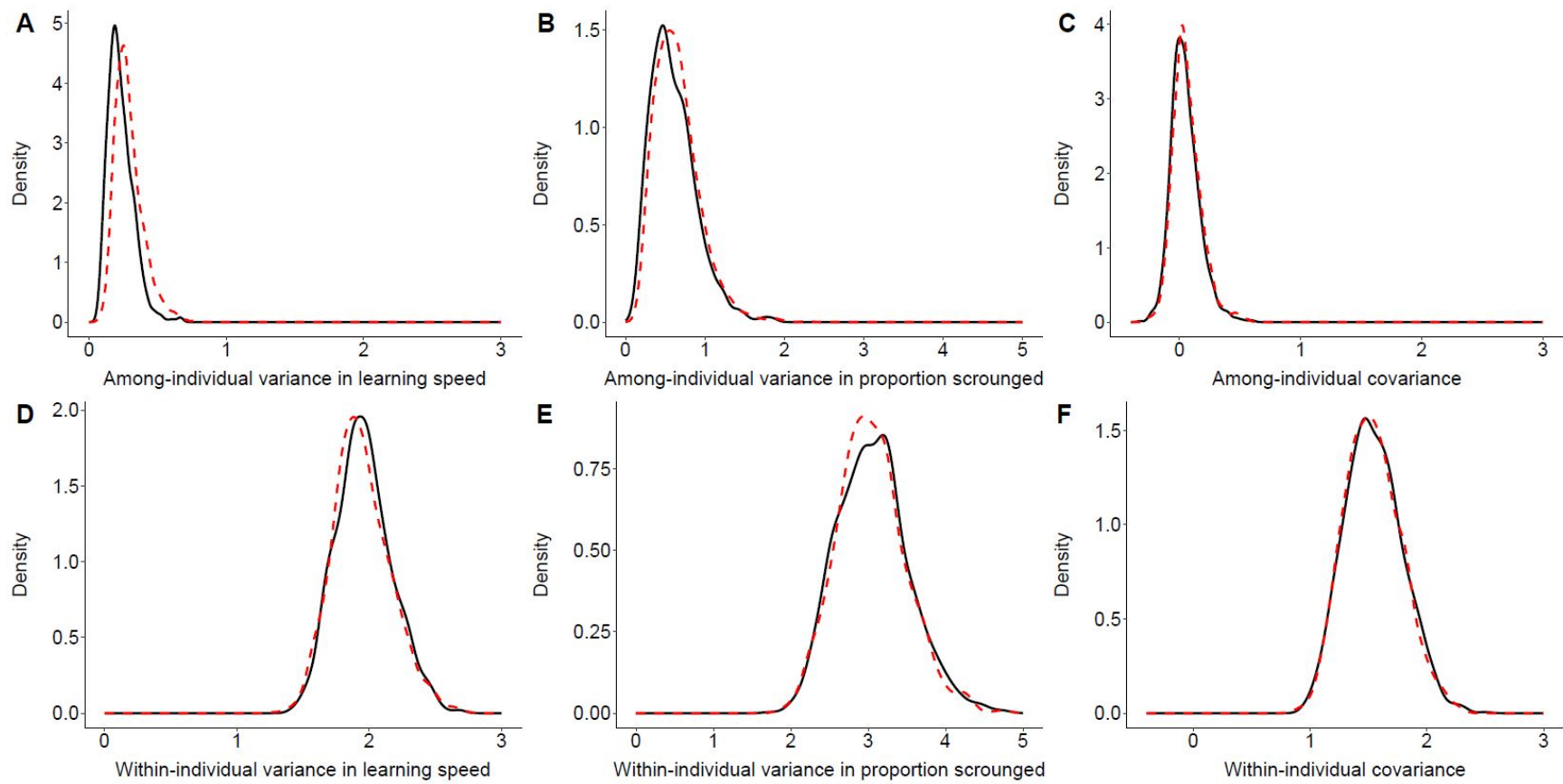


Figure S4. Posterior densities for among- and within individual covariation in proportion scrounged and learning speed in great tits. Posterior modes and 95% HPD intervals are given in Table 4 in the main text. Solid black line is for models calculated with an inverse gamma prior, as reported in the main text. Dotted red line is for models calculated with an alternative, inverse Wishart prior, as in Table S4. Both priors returned very similar results. A. Among-individual variance in learning speed, B. Among-individual variance in proportion scrounged, C. Among-individual covariance between learning speed and proportion scrounged, D. Within-individual variance in learning speed, E. Within-individual variance in proportion scrounged, F. Within-individual covariance between learning speed and proportion scrounged.

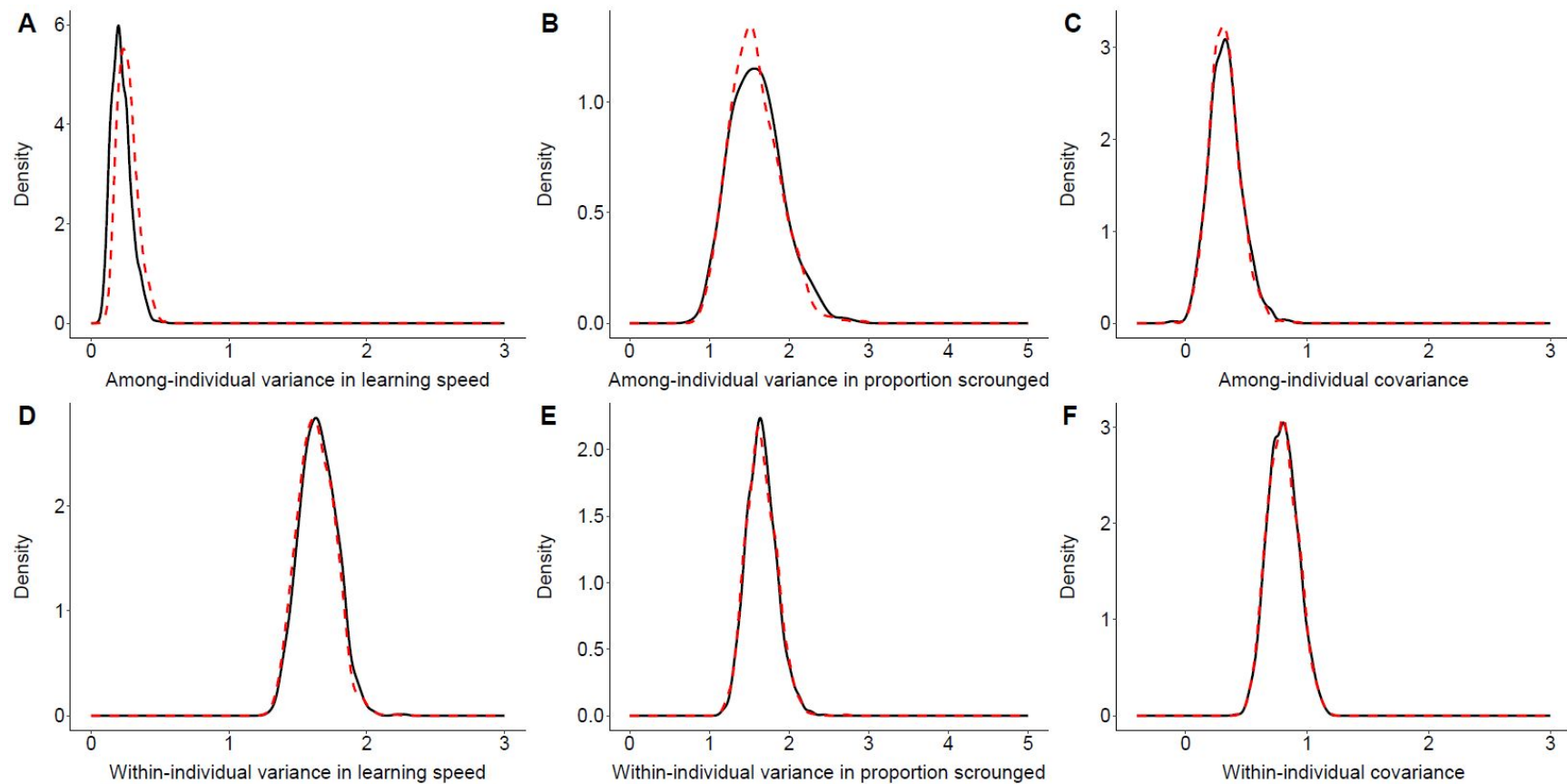


Figure S5. Posterior densities for among- and within individual covariation in proportion scrounged and learning speed in blue tits. Posterior modes and 95% HPD intervals are given in Table 4 in the main text. Solid black line is for models calculated with an inverse gamma prior, as reported in the main text. Dotted red line is for models calculated with an alternative, inverse Wishart prior, as in Table S4. Both priors returned very similar results. A. Among-individual variance in learning speed, B. Among-individual variance in proportion scrounged, C. Among-individual covariance between learning speed and proportion scrounged, D. Within-individual variance in learning speed, E. Within-individual variance in proportion scrounged, F. Within-individual covariance between learning speed and proportion scrounged.

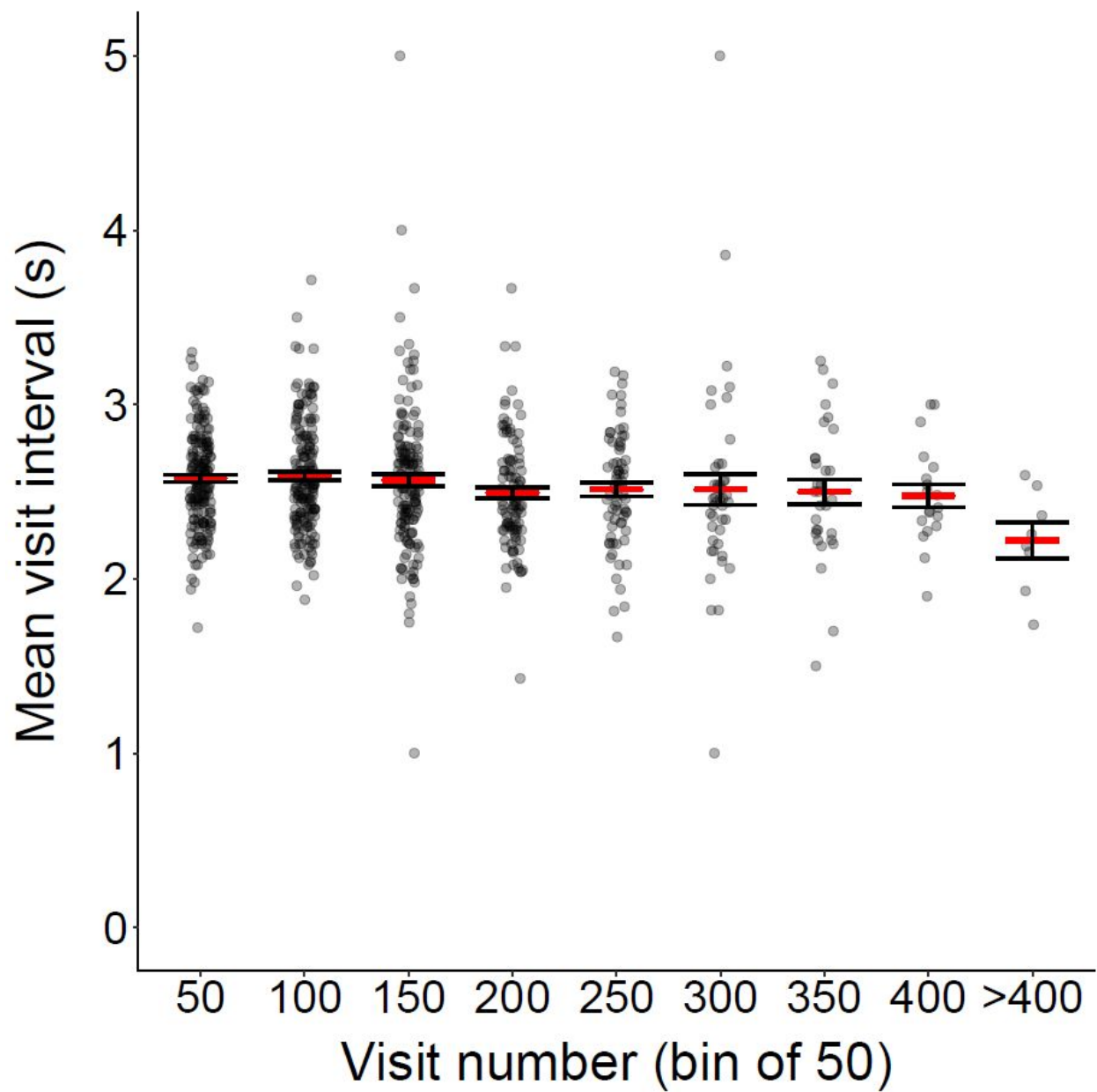
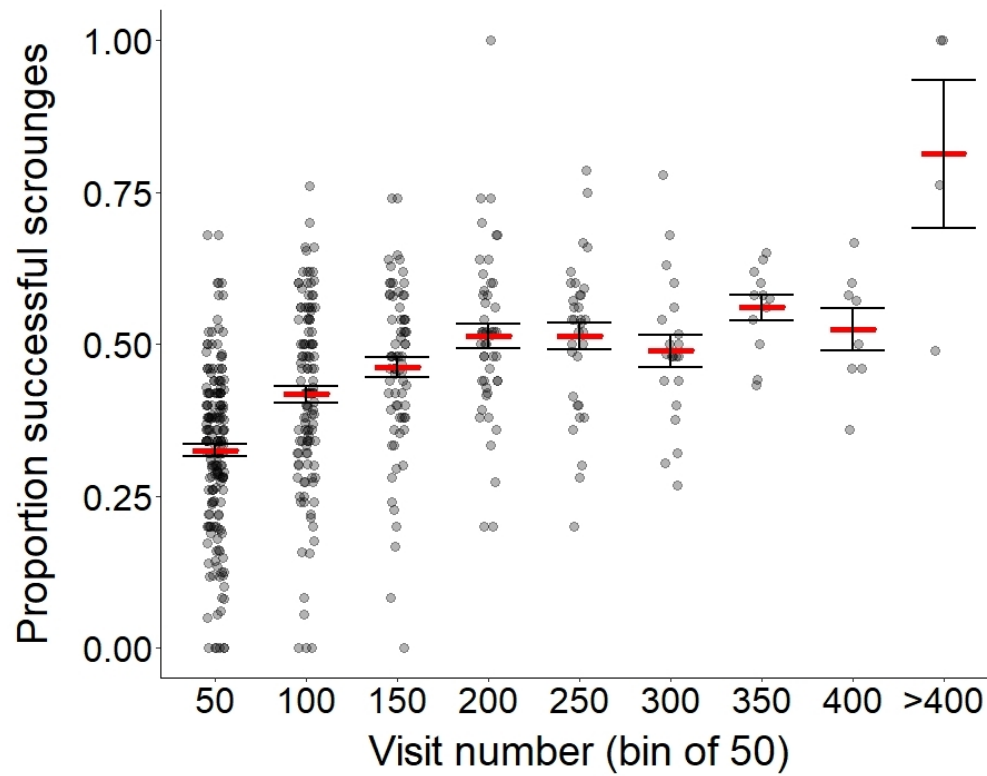


Figure S6. The relationship between visit number (only including produces) and the mean interval between a previous bird's visit and the producer's visit (only including intervals up to 5 s to be equivalent to the analyses in Figure 1B). See Figure 1B for additional details. Note that unlike Figure 1B, there is no strong decline in visit interval with increasing production visits, which suggests that there was not a general change in boldness, ruling out an alternative explanation for the pattern seen in Figure 1B.



Great tits and blue tits learned to improve their scrounging efficiency over time.

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