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Title: Among-trait covariance and cross-year repeatability for direct and indirect individual effects in producer–scrounger behaviour in wild house sparrows

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Abstract

Variation in social traits can be attributed to direct individual effects (DIEs) of the focal individual and indirect individual effects (IIEs) due to its social partners eliciting behavioural change, analogous to indirect genetic effects. Indirect effects affect the expressed phenotypic variation upon which selection can act, especially when they covary with direct effects, providing a potential explanation for slower or faster evolution than predicted by classic theory. However, little is known about the among-trait covariance of DIEs and IIEs, or whether IIEs are consistent across time and context and how this can affect evolutionary dynamics. Here we tested game theoretical predictions of producer-scrounger tactic use during social foraging games within a DIE-IIE framework in wild house sparrows (*Passer domesticus*). We used automated high-throughput phenotyping, where we assayed individuals repeatedly against different social partners. We provide evidence for small IIEs in producer-scrounger behaviour, and show high cross-year consistency. We found tight among-trait covariance, which is expected to impose strong constraints on the evolution of the DIEs and IIEs. Indirect effects decreased the potential heritable variation in producing and scrounging behaviour, which appear temporally stable. Overall, these effects may provide a potential mechanism for the long-term maintenance of stable social foraging strategies.

Introduction

A key feature of social interactions is that the optimal behaviour is often dependent upon the behaviour of social partners (McNamara & Weissing, 2010). The social environment consists of the phenotypes of social partners with which the focal individual interacts, and plays an essential role in the evolution of social phenotypes (Bergmüller & Taborsky, 2010; Wolf & McNamara, 2013).

Social evolution has long been modelled using evolutionary game theory within behavioural ecology, which aims to predict long-term evolutionary outcomes of frequency-dependent behavioural decisions (Maynard-Smith, 1984; McNamara & Weissing, 2010; McNamara & Leimar, 2020). Game theory utilises a cost-benefit approach in which the payoff of a given fitness currency depends upon the strategy employed by a social partner. The evolutionary outcome derived as a mathematical function of the payoff matrix yields a population equilibrium where all strategies perform equally well, referred to as the evolutionary stable strategy (ESS). Individuals can either adopt strategies that are tactically pure, mixed, or conditional where the employed tactic used is plastic, often relative to the phenotype of a social partner (Maynard-Smith, 1984; Giraldeau & Beauchamp, 1999; Tomkins & Hazel, 2007; McNamara & Weissing, 2010; McNamara & Leimar, 2020). Different individuals should opt for conditional tactic use that maximises their individual-specific payoffs, which may give rise to more-or-less responsive versus unresponsive strategies within the same population (Wolf *et al.*, 2008).

Another approach to studying social evolution comes from quantitative genetics, which provides a statistical framework to estimate short-term evolutionary consequences of social interactions (Hadfield & Thomson, 2017). A significant insight from quantitative genetics theory is that plastic phenotypes interact due to indirect genetic effects (IGEs) (Griffing, 1967; Moore *et al.*, 1997). In IGEs, genetic variation of a focal individual's phenotype 'impacts' or modifies their social partners' phenotype. In addition to this, the usual direct genetic effects (DGEs) of the focal individual's own genes determine its phenotype, and equate to additive genetic variance. At the phenotypic level, such direct and indirect effects have been referred to as direct individual effects (DIEs) and indirect individual effects (IIEs), and consist of both additive genetic variance and permanent environment effects (Han *et al.*, 2018). Indirect effects can have consequences for the amount of phenotypic and thus genetic variation that is expressed within a population on which selection can subsequently act, especially when they covary with direct effects (Wolf *et al.*, 1998; Bijma *et al.*, 2007b; McGlothlin *et al.*, 2010). This is because the heritability of traits with indirect effects is a function of both the direct and indirect effect variances, and their covariances (Bijma *et al.*, 2007a; b). Consequently, indirect effects can thus increase or decrease the total amount of heritable variation (τ^2), providing an appealing explanation for faster or slower evolution than predicted by classic theory (Wolf *et al.*, 1998; Bijma *et al.*, 2007b; McGlothlin *et al.*, 2010). For example, Wilson et al. (2009) found both direct and indirect effects on aggression in deer mice (*Peromyscus maniculatus*). These were shown to be heritable, with positive covariance between the propensity to be aggressive (DIE) and aggression elicited in social partners (IIE), increasing the total heritable variation for aggressive behaviour and accelerating the predicted rate of evolution. On average, IGEs explain 3% of the total phenotypic variation, and the effects are stronger in behavioural traits with 6%. Overall, IGEs tend to increase the total heritable variation, and therefore constitute a relevant phenomenon in social evolution (Santostefano *et al.*, 2024).

Empirical interest in indirect effects has greatly increased over the past decade (Bailey & Desjonquères, 2022). However, estimates in wild populations are limited and insights into the mechanisms of indirect effects are lacking. For instance, indirect effects are typically studied for one trait in isolation. However, social traits are often multivariate and depend upon multiple aspects of a social interaction. This multivariate nature of indirect effects has been acknowledged theoretically but has been neglected empirically (Moore *et al.*, 1997; Marie-Orleach *et al.*, 2017; Bailey *et al.*, 2018; Bailey & Desjonquères, 2022). Among-trait covariance can pose constraints on the trajectories of evolutionary responses due to genetic architecture and mechanistic constraints (Hansen & Houle, 2008). For instance, covariance between average level behaviours at the among-individual level, also referred to as 'behavioural syndromes', constrain potential evolutionary responses by 33% on average (Dochtermann & Dingemanse, 2013). In the context of indirect effects, phenotypic variation can be decomposed into its direct and indirect effects, which can covary within the same trait. From a multivariate perspective, direct and indirect effects can thus covary within and across traits. For instance, Santostefano et al. (2017) demonstrated in field crickets (*Gryllus campestris*) that aggression elicited in others (IIE) positively correlates with exploration behaviour (DIE). However, whether indirect effects covary across multiple traits has received little attention. Based upon the sign of the DGE-IGE relationship, this could either imply that certain individuals 'impact' or elicit more behavioural change in others across multiple traits, or that individuals elicit behavioural change in one trait but not in other traits. Such consistent individual differences in behaviour elicited in others parallel the different 'types' in the 'animal personality' or 'coping style' literature, as well as individual differences in strategies within game-theory (Wolf & Weissing, 2012). Furthermore, we have insufficient evidence whether individual variation in indirect effects is consistent across time and context, which will determine whether indirect effects modulate the amount of heritable variation. For example, if indirect effects are consistent across time and context, this implies that the consequences of indirect effects on heritable variation are consistent as well. Whereas if indirect effects are not consistent across time and context, this means that the modulatory effects are heterogeneous and fluctuate.

Game theoretical approaches in behavioural ecology and IGE models in quantitative genetics provide complementary approaches to the study of social evolution, but greater integration of these two frameworks and their contrasting timescales will yield an improved understanding of the evolution of social phenotypes (Abrams *et al.*, 1993; Araya-Ajoy *et al.*, 2020; McGlothlin *et al.*, 2022). Game theoretical models, such as producer-scrounger games (Barnard & Sibly, 1981), provide fruitful testing grounds to verify hypotheses about indirect effects. This is because game theoretical models make implicit predictions about the phenotypes that individuals should express as a function of their social environment (Barnard & Sibly, 1981; Giraldeau & Beauchamp, 1999). In other words, they contain implicit assumptions about indirect effects that can be tested empirically. This has been approached from a theoretical modelling perspective (Trubenová *et al.*, 2015; McGlothlin *et al.*, 2022), however we still lack empirical studies that incorporate IGEs into game theoretical scenarios.

The producer-scrounger social foraging game provides an appropriate experimental system because individuals can repeatedly be assayed when playing with different social partners, allowing for the estimation of both direct and indirect effects. Here individuals can opt for two mutually exclusive behavioural tactics, where individuals either ‘produce’ and sample the environment and search for resources individually, or ‘scrounge’ where they (search for opportunities to) exploit resources found by producers (Barnard & Sibly, 1981). Producing and scrounging payoffs are negatively frequency-dependent, which means that each tactic has higher pay-offs when it is rarer in the population (Giraldeau & Beauchamp, 1999; Giraldeau & Caraco, 2000; Mottley & Giraldeau, 2000). Variance in social partner producing and scrounging will therefore affect the plastic expression of focal producing and scrounging, giving rise to indirect effects in producer-scrounger games. From an indirect effects perspective, the negative frequency-dependent nature of producer-scrounger interactions would imply that a higher degree of producing from an individual would elicit reduced producing and increased scrounging in its social partners. Since playing either tactic affects the payoffs and subsequent expression of the traits of both producing and scrounging, a multivariate scenario occurs in which the direct and the indirect effects in both producing and scrounging behaviours are expected to covary (i.e. a 4 x 4 matrix).

In this paper, we adopt a variance partitioning approach under the assumption of the phenotypic gambit to study direct and indirect individual effects (DIE & IIE) on the expression of producer-scrounger behaviour during social foraging under experimental social environments in wild Norwegian house sparrows (*Passer domesticus*) across two years. Our aims are as follows. 1) Estimate how repeatable the DIE and IIE in producing and scrounging behaviour are. We expected the repeatability of IIEs to be relatively low, based upon reports within the IGE literature (Santostefano *et al.*, 2024). However, that the IIEs would be relatively stronger compared to average estimates of behavioural IGEs, because IIEs also consist of permanent environment effects. 2) Estimate the temporal consistency (i.e. cross-year repeatability) in DIEs and IIEs in producing and scrounging behaviour. We predicted higher temporal consistency for DIEs, because social foraging strategies are expected to be individually stable across time, and lower consistency for IIEs as these are expected to be more context dependent and vary according to the social environment. 3) Estimate the covariance at the individual level between DIEs and IIEs across producing and scrounging behaviour. A negative covariance was expected between DIEs and IIEs for both producing and scrounging, based upon the negative frequency dependence inherent in the producer-scrounger game. We expected that individuals that produce more elicit more scrounging in their social partners and *vice versa* for individuals that scrounge more. 4) Do indirect effects in producing and scrounging behaviour affect the potential amount of heritable variation? Because we expected a negative covariance between the DIEs and IIEs, we predicted that the potential total heritable variation would be decreased by indirect effects.

Methods

Study population

We conducted social foraging experiments in wild house sparrow (*Passer domesticus*) flocks associated with five dairy farms within the Åfjord municipality in Norway. This meta-population has been monitored since 2012, with limited dispersal between farms. During the winter of 2022 we captured 168 sparrows, and in the winter of 2023 we captured 140, totalling 245 unique individuals. We caught sparrows within their home range using mist nets (3 – 18 m), with a total capture rate of 93.1%. Upon capture, we outfitted birds with unique combinations of an alphanumerical metal ring, colour-rings, and a passive integrated transponder (PIT) tag fitted in the colour ring on one of the tarsi (Dorset ID, Aalten, the Netherlands).

Housing & habituation

Captured birds were transported to an unused farm building on the island of Lauvøya (63°55'40.3"N, 9°55'51.7"E), where temporary aviaries and testing arenas were constructed out of wood, and tarpaulins. After capture, we fitted all individuals with QR-code barcode backpacks (see Alarcón-Nieto *et al.*, 2018) for identification during video analysis. These backpacks with six unique patterns were secured with elastic cord loops around each leg. We divided the birds into groups of six, based upon capture time, with the aim of an equal sex ratio of birds that were familiar to each other from the same farm. We supplemented 6 groups with 11 previously assessed individuals to form full groups. We housed groups in 2 x 1.5 x 2 m habituation aviaries provided with branches and nestboxes, *ad libitum* access to food and water, and maintained at an ambient temperature of 10°C (± 2), with a 14:10 light-dark cycle. Over the span of 3 days, we gradually trained the birds to forage on a dummy 'checkerboard' feeder - a platform with regularly-spaced 'wells' filled with sand to hide where the food was located (see Suppl. Figure 1). After completing the habituation procedure at the end of the afternoon on the third day, groups were caught via mist net by sluicing them into an adjacent aviary, and assigned a trial ID (A - F or G – L – see Suppl. Figure 2). We briefly housed the birds in individual wooden nestboxes, which allowed individuals to be moved between trial cages between successive trials. For the rest of the evening, we released the individuals in triads into the cages where the foraging experiments would occur, allowing them to habituate overnight. During the overnight habituation, the feeders were filled with 40 grams of millet seeds, divided among 28 wells, plus 8 wells containing only sand. The following day, all individuals within a group underwent social foraging trials in triads.

Experimental setup

The experiments took place on a 36-well checkerboard feeder, similar to the habituation feeders, but equipped with custom-made radio frequency identification (RFID) readers underneath each well to read PIT-tags (Dorset ID Aalten, the Netherlands). Each well had four RFID readers with a multiplexor system activating one reader at a time in a sequence, with cycles alternating approximately every half-second. This allows for the automatic tracking of individual arrival and departure times of visits to wells. Three separate checkerboard feeders were placed inside wire-mesh cage constructions (1 x 1.2 x 1 m) within an experimental aviary, and visually separated using tarpaulins (see Suppl. Figure 3). Each feeder was equipped with a perch, *ad libitum* access to water, and three openings for the individual nestboxes. GoPro Hero 8 cameras (1080p, 24 FPS on linear view) were mounted on top of the feeder cages for the purpose of video recording (see: Video analysis).

Producer-scrounger trials

We conducted producer-scrounger trials, while continuously altering the social environment for each focal individual across trials. With groups of six birds, 20 unique triadic combinations were possible, in which each focal individual plays 10 times with different social partners. All 20 unique combinations were played in one day, and we repeated all combinations on a second consecutive trial day. Per trial day, we randomised the order of the unique combinations, and we allocated the randomised combinations evenly over the three checkerboard feeders based on six predefined patterns (see Suppl. Figure 2). In 2023, for some of the groups we also performed full group trials using all six individuals during one day for the purposes of another experiment. Half of these groups had the group trial prior to the triadic trials and the other half after the triadic trials.

Each triadic trial lasted 15 minutes with a 25-minute resting period between trials, starting at approximately 08:20 and ending at 17:35. Up to three trials ran simultaneously, with three birds within a group resting in their individual nestboxes during every other trial cycle to prevent satiation and to maintain foraging motivation (see Suppl. Figure 2). For every trial, we refilled the interchangeable well cups (2.7 x 3.6 cm, 17.5 ml) with fine sand. We baited 14 out of 36 wells with 12 grams of millet equally divided over the wells. The seeds were covered with approximately 1 cm of sand filled up to 85% (±5) capacity, so all wells looked indistinguishable. The checkerboard feeders were filled according to predefined randomised patterns, determined by two dice rolls, selecting both the pattern and its orientation (see Suppl. Figure 4). Trials started by turning on the camera and recording a reference PIT-tag on the checkerboard feeder to mark the start of the trial. We stopped the trials after 15 minutes, and flushed each bird separately into an individual nestbox and shut in via sliding doors controlled by a pulley mechanism. After capture, the birds were identified with an ARE-H5 PIT-tag hand scanner (AEG-ID, Ulm, Germany) and their corresponding trial ID label was assigned, and they were redistributed for the next trial. Between trials, we cleaned the feeder plates with wet wipes, and we collected any remaining sand and seed from the plate and wells in a bucket. We sieved the collected material and discarded anything other than seeds by use of tweezers. The remaining seeds were weighed to the nearest 0.05 gram.

We repeated this process for each trial cycle within a day. Afterwards, the checkerboard feeder was prepared for the overnight habituation as described previously, so that individuals could stay in the checkerboard feeder cages for a new set of trials on the following day. If two groups had overnight habituation, one of the triads from the initial group was housed in a dummy setup. After completing the second day of trials, the QR-code backpacks were removed and we released the birds into a final aviary (10 x 5 x 2 m), where they were monitored for health before being released at the site of capture within maximally 14 days after capture.

Video analysis

In order to calibrate the behaviours derived from the RFID checkerboard feeder, we annotated behaviours by means of video analysis in BORIS (V 7.13.6; Friard & Gamba, 2016). We randomly sampled 112 videos from the 2022 dataset with a stratified design, selecting one trial per group for each trial day (e.g. ABC) along with its complementary trial codes (e.g. DEF), resulting in four annotated trials per group with two observations per individual. For each trial video, we observed all three individuals during separate viewings as focal for the whole 15 minutes. Focal individuals were distinguished using their unique QR code backpack within a group. Foraging behaviours were scored based on visits to wells. Visits were labelled as ‘producing events’ when individuals found and consumed food from an unoccupied baited well, and as ‘scrounging events’ when individuals joined occupied baited wells and consumed seeds (see Beauchamp & Giraldeau, 1997; Beauchamp, 2001; Lendvai *et al.*, 2004; Katsnelson *et al.*, 2008; Tóth *et al.*, 2009; Morand-Ferron & Giraldeau, 2010a; Belmaker *et al.*, 2012; Ilan *et al.*, 2013, and Suppl. Table 1 for the used ethogram). Before starting the video analysis, we established inter- and intra-observer reliability. All observers scored the same three 3-minute video clips of trials (that were not scored in the actual analysis), repeated three times across observers. Observer reliabilities were estimated with the IRR package (Gamer *et al.*, 2019) in R (V4.3.1 R Core Team, 2023). We maintained or exceeded inter- and intra-observer reliability thresholds of 0.85 for scrounging behaviour and 0.9 for all other behaviours (Suppl. Table 1).

RFID measures of producing-scrounging behaviour & calibration

In order to derive behavioural measures from the RFID checkerboard feeder, we labelled reads recorded at unique wells as visits with a start and stop time per trial, and individual identity. In this process, we omitted single read visits with a visit duration of zero, because of their uninformative nature. We derived variables from the RFID data that were used to conditionally label visits as ‘producing’ or ‘scrounging’ events at baited wells. We performed sliding window analyses to infer whether multiple tags were read at the same well at -3, -1, 0, +1 seconds per second per individual. We labelled visits as ‘producing’ events if: 1) the well was baited with seeds; 2) no other tags than the focal were read at the start (-1, 0, +1 seconds) of the visit nor 3 seconds prior to the visit; 3) millet seeds were consumed within the trial, based on the weight of remaining seeds; and 4) the visit lasted longer than 5 seconds. We labelled visits as ‘scrounging’ events if: 1) more than one tag was read at the start of the visit or a tag was read 3 seconds prior to the visit; 2) the social partner has been at the well for at least three seconds; 3) the well was produced at previously; and 4) the focal visit had more than 5 reads. The number of producing and scrounging events per trial and individual were summed to yield the number of occurrences per trial per individual.

The annotated video data were used to calibrate the accuracy of the RFID-system derived producing and scrounging behaviour. We performed Pearson's correlations with the number of observed and derived producing and scrounging events per individual within a trial. We found Pearson correlations of 0.70 for producing visits and 0.70 for scrounging visits within a trial per individual. To verify whether the relationship found between the RFID derived behaviour and the annotated video data was generalizable, we scored an additional 68 videos from the 2023 dataset following the same stratified sampling design. Here, we consider the 2022 video dataset as the training dataset and the 2023 video dataset as the testing dataset. We fitted linear models with the annotated video data as the response variable and the derived RFID behaviours as a covariate, the year as a fixed effect and an interaction between year and the RFID-derived behaviour. We found that there was no significant difference between the sampled datasets, indicating consistent assignment of RFID-derived behavioural data. Overall, when fitting the full 2022 and 2023 dataset we found a Pearson's correlation of 0.67 for producing behaviours and 0.72 for scrounging behaviours per individual within a trial.

During the video analysis, we noticed that baited wells were almost never fully depleted by the individual that first 'produced' at the well, or when a well was then 'scrounged' upon by another individual. Consequently, individuals would return to already produced wells. Returning to wells that were previously produced or scrounged at are not really covered by producing-scrounging theory thus far, and such return events are less informative than the primary producing or scrounging visits per well. Therefore, for the purposes of the current analyses, we used only primary visits per well to estimate how often an individual employed a certain social foraging strategy to obtain resources within a trial.

Statistical analyses

In total, 1160 triadic trials were conducted in 2022, and 960 trials in 2023, providing a total of 2120 trials. Each trial contributes data on 3 focal individuals, because every individual plays as both a focal individual and as social partner for the two other social partners (Santostefano *et al.*, 2016). Therefore, our dataset includes 6360 observations over 2120 trials. Of these, we only included observations in our analyses where all three individuals were registered on the checkerboard feeder during a trial, and focal individuals had non-zero producing or scrounging events, resulting in 5108 observations. These observations where individuals did not play the game are likely due to habituation effects to the experimental setup. We fitted linear mixed-effect models in a Bayesian framework using Stan (V 2.32.2 Stan Development Team, 2024) within R (V4.3.1 R Core Team, 2023). We fitted models with Gaussian likelihood functions with 4 chains, 2000 warm up iterations and 3000 sampling iterations, with a thinning interval of one. We set weakly informative priors with Gaussian distributions ($\mu = 0$, $\sigma = 5$) for fixed effects, half exponential distributions ($\lambda = 3$) for random effects, and LKJ distributions ($\eta = 3$) for correlations. We estimated and report the posterior medians with a 95% credible interval (Pick *et al.*, 2023). We performed posterior predictive checks with the ShinyStan package (Stan Development Team, 2017), and found proper convergence of the chains.

Univariate phenotypic models

First, we fitted 14 univariate mixed-effect models for producing and scrounging events per trial per individual. We fitted these models split per year (e.g. 2022), year and trial day (e.g. trial day1 in 2022), and with the full dataset, to assess potential differences in mean level behaviour, individual variation in DIEs and IIEs and correlation structure between the DIE and IIE across these temporal levels (see Suppl. Mat Text1. and Suppl. Table 2 & 3 for more information).

Bivariate phenotypic models

Second, we fitted a bivariate mixed-effect model to estimate the patterns of (co)variance between the DIE and the IIE for producing and scrounging at the individual level. We fitted producing and scrounging events per trial per individual as response variables, and Focal ID and social partner IDs as random effects to partition the direct individual effect (DIE) and indirect individual effect (IIE), and their covariance (McGlothlin & Brodie III, 2009; Han *et al.*, 2018). Variance due to social partner IDs (IIE) was constrained to be equal, since the assignment of social partner IDs was arbitrary. To account for our study design, we fitted (triadic) trial day (0 - 1), individual trial order (1 - 10), and whether individuals participated in larger groups trials prior to the triadic trials (0 - 1), as fixed effects, and TrialID (n = 1997), and GroupID (n = 53) as random effects. Trial order, and trial day were mean centred such that the intercept was estimated for the average trial for an individual. We fitted a three-way interaction between trial day, trial order and participation in larger group trials, to account for habituation effects during the trials. Since we decompose both producing and scrounging behaviour into direct (DIE) and indirect effects (IIE), a 4 x 4 P-matrix was constructed to estimate the six covariances and correlations between DIEs and IIEs effects across producing and scrounging behaviour. The bivariate model provided similar estimates as the full univariate models (Suppl. Table 2 & 3) and provided unbiased estimates compared with 50 simulated datasets with the same data structure (see Suppl. Figure 5).

For all random effects, we estimated adjusted repeatability and unadjusted repeatability by fitting a model with and without the fixed effect structure respectively (Suppl. Mat Text2). We estimated the total social phenotypic effect of producing and scrounging behaviour according to Bijma et al. (2007b) equation 6 (Suppl. Mat Text3). This is analogous to the total heritable variation (τ^2), but at the phenotypic level ($P\tau^2$), which theoretically sets the upper bound for τ^2. We did not adjust for trial-level group size effects for the covariance with IIEs, because our interest lies in how a focal individual impacts one social partner on average. Note that the model yields an estimate of the among-individual variance in IIEs for focal individuals. This is not the same as the total variance in (focal) phenotype attributable to IIEs, because within each trial, a focal individual experiences the IIEs of both of its social partners. Therefore, to obtain the total IIE variance for the total phenotypic variation, we multiplied the IEE variance by two (Bijma *et al.*, 2007b).

Cross-year repeatability

In order to estimate temporal consistency, we fitted univariate models to estimate short-term and cross-year repeatability for the DIEs and IIEs of producing and scrounging behaviour. For this, we fitted two additional random effects comprised of unique indices for the combinations of year and individual ID for both the focal and the social partners. We estimated short-term and cross-year repeatability based on equations 3a and 5 described by Araya-Ajoy et al. (2015), for the intercept of the DIE and the IIE, and its respective year-ID series variance (see Suppl. Mat text2).

Results

Fixed effects

On average individuals performed 1.55 producing events and 0.64 scrounging events per trial (Table 1). This implies that during the average 15 min trial there were approximately 4 producing events and 2 scrounging events per triad. Producing and scrounging behaviour both increased as a function of trial order, but scrounging decreased slightly between years and trial days. Individuals that participated in full group trials prior to the triadic trials did not produce or scrounge more or less. The three-way interaction between individuals that were involved in full group trials before the triadic trials, trial day and trial order affected scrounging , but not producing behaviour. Two-way interactions also did not affect producing behaviour.

Table 1: Posterior medians with 95% credible intervals (in parentheses) for the full and unadjusted bivariate models for the direct individual effect (DIE) and indirect individual effect (IIE) in producing and scrounging behaviour. The DIE represents the average level behaviour of the focal and the IIE represents the behaviour elicited in others as a social partner. Pτ2 refers to the social phenotypic variance attributable to interacting phenotypes. Note that the covariances and correlations are reported in Figure 1.

Variables	*Producing*	*Scrounging*	*Producing unadjusted*	*Scrounging unadjusted*
Fixed effects	*β (95% CI)*	*β (95% CI)*	*β (95% CI)*	*β (95% CI)*
Intercept	*1.545 (1.465 ; 1.623)*	*0.640 (0.596 ; 0.685)*	*1.530 (1.451 ; 1.613)*	*0.656 (0.614 ; 0.697)*
Year	*-0.119 (-0.251 ; 0.014)*	*-0.085 (-0.161 ; -0.010)*	-	-
Trial order	*0.030 (0.018 ; 0.042)*	*0.019 (0.011 ; 0.027)*	-	-
Trial day	*0.065 (-0.001 ; 0.133)*	*-0.047 (-0.093 ; 0.000)*	-	-
Group trial before	*-0.200 (-0.414 ; 0.011)*	*0.102 (-0.021 ; 0.221)*	-	-
*Trial day * Group trial before*	*-0.176 (-0.364 ; 0.014)*	*-0.035 (-0.098 ; 0.029)*	-	-
*Trial day * Trial order*	*-0.018 (-0.041 ; 0.005)*	*-0.022 (-0.039 ; -0.006)*	-	-
*Trial order * Group trial before*	*-0.020 (-0.052 ; 0.012)*	*0.003 (-0.043 ; 0.050)*	-	-
*Trial day * Trial order * Group trial before*	*0.007 (-0.057 ; 0.070)*	*0.053 (0.008 ; 0.099)*	-	-
Random effects	*σ^2 (95% CI)*	*σ^2 (95% CI)*	*σ^2 (95% CI)*	*σ^2 (95% CI)*
DIE	*0.328 (0.263 ; 0.410)*	*0.103 (0.080 ; 0.131)*	*0.328 (0.264 ; 0.410)*	*0.103 (0.081 ; 0.131)*
IIE	*0.020 (0.013 ; 0.033)*	*0.020 (0.014 ; 0.028)*	*0.020 (0.011 ; 0.031)*	*0.021 (0.014 ; 0.029)*
Trial	*0.034 (0.020 ; 0.050)*	*0.048 (0.036 ; 0.061)*	*0.039 (0.023 ; 0.056)*	*0.051 (0.039 ; 0.066)*
Group	*0.025 (0.003 ; 0.058)*	*0.003 (0.000 ; 0.016)*	*0.041 (0.019 ; 0.077)*	*0.003 (0.000 ; 0.016)*
Residual	*1.139 (1.093 ; 1.186)*	*0.486 (0.465 ; 0.508)*	*1.140 (1.095 ; 1.186)*	*0.486 (0.465 ; 0.508)*
total phenotypic effect	*0.150 (0.091 ; 0.228)*	*0.048 (0.018 ; 0.081)*	*0.142 (0.086 ; 0.219)*	*0.052 (0.019 ; 0.087)*
Total	*1.570 (1.486 ; 1.669)*	*0.681 (0.647 ; 0.720)*	*1.591 (1.506 ; 1.694)*	*0.686 (0.653 ; 0.725)*
Repeatability	*R (95% CI)*	*R (95% CI)*	*R (95% CI)*	*R (95% CI)*
DIE	*0.209 (0.174 ; 0.249)*	*0.151 (0.121 ; 0.185)*	*0.207 (0.172 ; 0.246)*	*0.150 (0.121 ; 0.185)*
IIE	*0.013 (0.008 ; 0.020)*	*0.029 (0.020 ; 0.040)*	*0.012 (0.007 ; 0.019)*	*0.030 (0.020 ; 0.041)*
Trial	*0.022 (0.013 ; 0.032)*	*0.070 (0.053 ; 0.089)*	*0.024 (0.015 ; 0.035)*	*0.075 (0.057 ; 0.095)*
Group	*0.016 (0.002 ; 0.036)*	*0.005 (0.000 ; 0.022)*	*0.026 (0.012 ; 0.048)*	*0.005 (0.000 ; 0.024)*
Residual	*0.725 (0.684 ; 0.762)*	*0.713 (0.675 ; 0.748)*	*0.716 (0.675 ; 0.753)*	*0.708 (0.670 ; 0.742)*
total phenotypic effect	*0.095 (0.059 ; 0.143)*	*0.071 (0.028 ; 0.118)*	*0.089 (0.054 ; 0.135)*	*0.075 (0.028 ; 0.126)*

Repeatability & variances

The total phenotypic variance in producing was 1.570, and 0.681 for scrounging behaviour (Table 1). The direct individual effect (DIE), or average level behaviour, had moderate and low repeatability, where 20.9% of the variance in producing behaviour and 15.1% of the variance in scrounging behaviour was attributable to differences among focal individuals (Table 1 & Figure 1). The indirect individual effect (IIE), representing the behavioural change elicited in others, had low repeatability, where 1.3% of the variance in producing behaviour and 2.9% of the variance in scrounging behaviour was attributable to the focal individual. The amount of variance in producing and scrounging behaviour caused by interacting with both social partners within a trial was 2.6% and 5.8% respectively. The variation among groups was close to zero for both producing and scrounging behaviour, indicating no bias in group formation. Scrounging behaviour varied more among trials than producing behaviour. Residual variance was high for both producing and scrounging behaviour, which must be partially due to measurement error from the RFID system. The adjusted repeatability estimates did not deviate much from the unadjusted repeatability estimates (see Table 1), further showing that the fixed effects structure of the model only explained a small amount of variance.

A

Σ_i	*Producing DIE*	*Producing IIE*	*Scrounging DIE*	*Scrounging IIE*
Producing DIE	0.328 (0.263 ; 0.410)	-0.051 (-0.071 ; -0.036)	-0.138 (-0.178 ; -0.106)	0.062 (0.046 ; 0.082)
Producing IIE	-	0.020 (0.013 ; 0.033)	0.040 (0.028 ; 0.056)	-0.013 (-0.021 ; -0.007)
Scrounging DIE	-	-	0.103 (0.080 ; 0.131)	-0.041 (-0.054 ; -0.030)
Scrounging IIE	-	-	-	0.020 (0.014 ; 0.028)

B

Ω_i	*Producing DIE*	*Producing IIE*	*Scrounging DIE*	*Scrounging IIE*
Producing DIE	0.209 (0.174 ; 0.249)	-	-	-
Producing IIE	-0.800 (-0.934 ; -0.606)	0.013 (0.008 ; 0.020)	-	-
Scrounging DIE	-0.754 (-0.830 ; -0.655)	0.896 (0.752 ; 0.975)	0.151 (0.121 ; 0.185)	-
Scrounging IIE	0.775 (0.629 ; 0.895)	-0.663 (-0.877 ; -0.414)	-0.747 (-0.905 ; -0.583)	0.029 (0.020 ; 0.040)

D

Σ	*Residual producing*	*Residual scrounging*
Residual producing	1.139 (1.093 ; 1.186)	-0.294 (-0.318 ; -0.271)
Residual scrounging	-	0.486 (0.465 ; 0.508)

E

Ω	*Residual producing*	*Residual scrounging*
Residual producing	0.725 (0.684 ; 0.762)	-
Residual scrounging	-0.396 (-0.423 ; -0.369)	0.713 (0.675 ; 0.748)

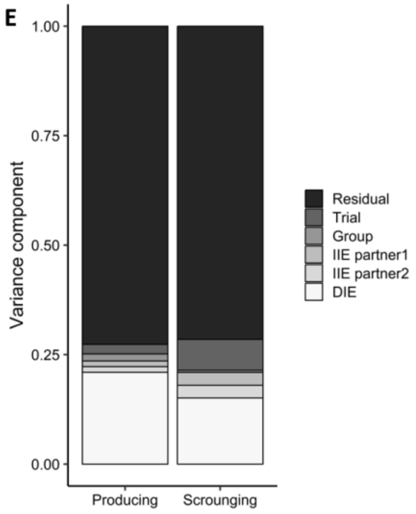

Figure 1: (A) Variance-covariance matrix showing the variances on the diagonal and the covariances above the diagonal for the direct individual effect (DIE) and the (social) indirect individual effect (IIE) for producing and scrounging behaviour. (B) Correlation matrix showing the repeatabilities on the diagonal and the correlations below the diagonal for DIEs and IIEs. (C) Stacked bar plot of the variance components for producing and scrounging behaviour. Trial represents the variance attributed to variation among the 15-minute triadic trials, and group represents the variance among the groups of six individuals. Note that the IIE variances are presented for both social partners. (D) Residual variance covariance matrix showing the variances on the diagonal and the residual covariance above the diagonal. (E) Residual correlation matrix showing the variance components on the diagonal and the residual correlation below the diagonal.

Temporal consistency

The univariate cross-year repeatability models provide evidence for high cross-year repeatability of the DIE and the IIE for producing and scrounging behaviour (Figure 2, Suppl. Table 4). The long-term repeatabilities were similar to the bivariate model estimates, and hence are not reported here (Suppl. Tables 2-4). For producing behaviour, the individual cross-year repeatability for the DIE was 0.693, and 0.745 for the IIE. Similarly, for scrounging the individual cross-year repeatability for the DIE was 0.794, and 0.633 for the IIE. These high cross-year repeatability estimates indicate that individuals exhibited similar mean level behaviours, and elicited similar levels of behavioural change in others across years.

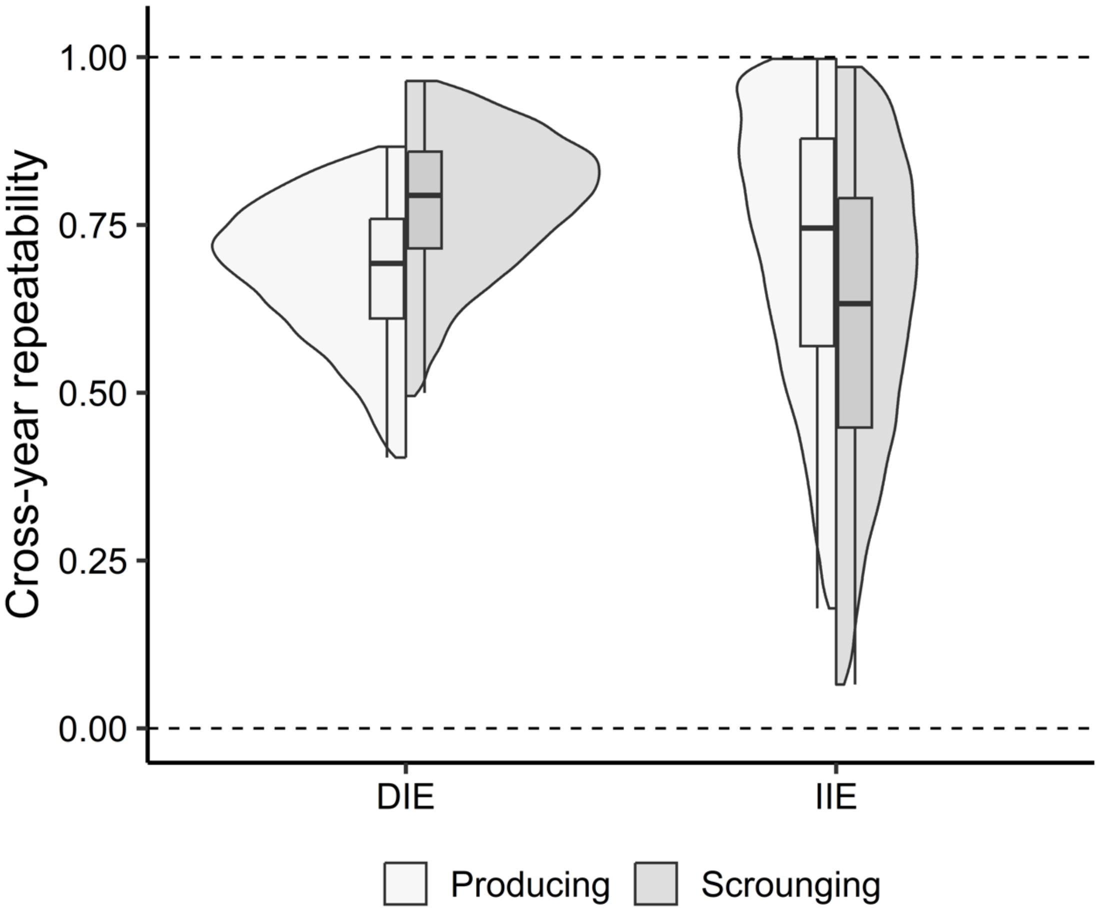

Figure 2: Half violin plot depicting the cross-year repeatability of producing and scrounging behaviour for the direct individual effect (DIE) and indirect individual effect (IIE). The boxplot shows the median (horizontal line), and interquartile range (box), and the violin shows the posterior distribution as a density function (N.ind = 245, N.repeats = 63, N.obs = 5108, N.series = 307).

Phenotypic among trait covariance & correlations

The bivariate mixed model provides strong evidence for a tight phenotypic among-trait covariation for DIEs and IIEs at the individual level (Figures 1 & 3). The model shows that individuals with a higher tendency to produce elicited less producing in other individuals, elicited more scrounging in others, and had a lower propensity to scrounge themselves. Furthermore, individuals that scrounged more on average elicited more producing in others, but less scrounging behaviour in others. Individuals that elicited more producing elicited less scrounging in their social partners, and *vice versa*. The residual or within-individual correlation was negative, which implies that within a given trial when individuals produce more than average they scrounge less than average, and *vice versa*.

The total social phenotypic effect ($P\tau^2$), which is the proportion of phenotypic variance attributable to interacting phenotypes, for producing was 0.095, and 0.071 for scrounging behaviour (Table 1). This implies that phenotypic variation or the upper limit of the potential heritable variation due to social effects was 9.5% in producing behaviour and 7.1% in scrounging behaviour, which was 54.5% and 53% lower, respectively, compared with the repeatability of the DIEs.

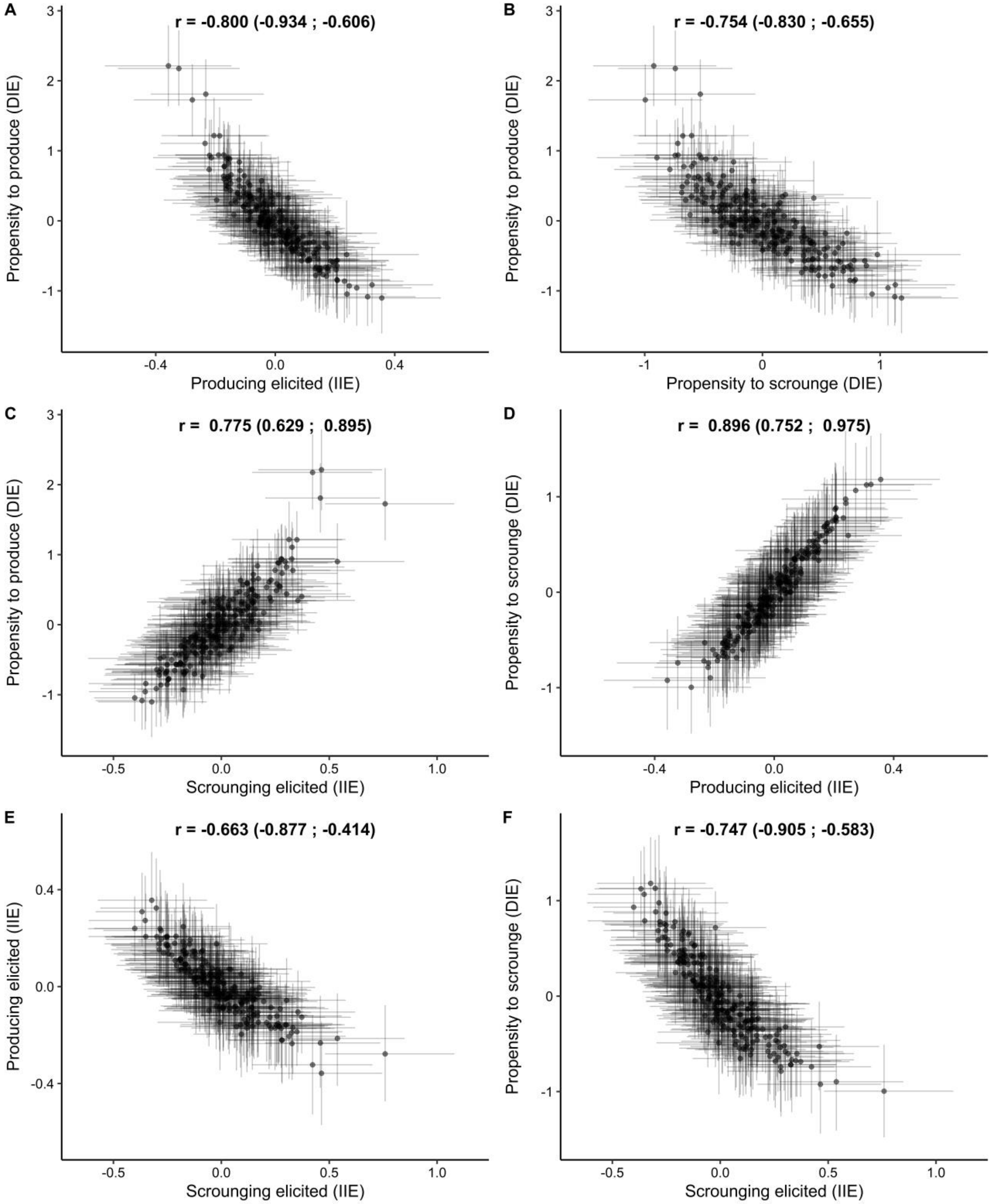

Figure 3: Posterior median of Best Linear Unbiased Predictors (BLUPS) with 95% credible intervals at the individual level (N.ind = 245, N.obs = 5108), as a visualization of the correlation structure across the direct individual effect (DIE) and the indirect individual effect (IIE) in producing and scrounging behaviour. A) Producing DIE - producing IIE. B) Producing DIE - scrounging DIE. C) Producing DIE - scrounging IIE. D) Scrounging DIE - producing IIE. E) Producing IIE - scrounging IIE. F) Scrounging DIE - scrounging IIE.

Discussion

In this study, we show evidence for both indirect individual effects (IIE) in the behavioural change elicited in others, and for direct individual effects (DIE) in the average behaviour in social foraging. The IIEs explained a small amount of variation in producing and scrounging behaviour, but they were highly consistent across years. The DIEs showed moderate repeatability, but showed high temporal consistency across years. We also found a high degree of covariance between the DIEs and IIEs across and within producing and scrounging behaviours at the individual level. We found that individuals that produce more scrounge less, providing evidence for purer producer-scrounger strategies. Despite these small indirect effects, they still have the potential to decrease the amount of phenotypic variation. To our knowledge, this is the first empirical study that shows among-trait covariance of DIEs and IIEs across multiple behaviours with high temporal consistency.

We derived our measurements of producing and scrounging behaviour via a high throughput RFID system. Based on the correlations of around 0.7 with observed data, we are aware that our RFID data contains reasonable measurement error that is currently unquantifiable. We therefore have to consider that the residual variance of our models would have been inflated by measurement error and that any repeatability estimates here may in fact be underestimated as a result (Nakagawa & Schielzeth, 2010).

Repeatability of the DIEs & IIEs

We found moderate to low repeatabilities (R = 0.209 & 0.151) in producing and scrounging behaviour respectively. Other studies that estimated among-individual variation in producing and scrounging behaviour found varying repeatability that ranged from 0.37 to 0.5 for producing, and 0.06 to 0.5 for scrounging behaviour (David *et al.*, 2014; Aplin & Morand-Ferron, 2017; Barou-Dagues *et al.*, 2020; Reichert *et al.*, 2021). Repeatability is generally lower for traits that are very labile and affected by energetic state and the social environment (Bell *et al.*, 2009; Santostefano *et al.*, 2016), which applies to social foraging tactic use, especially under variable social environments, similar to our experimental setup. For instance, sticklebacks (*Gasterosteus aculeatus*) that were socially housed show lower repeatability in boldness than when housed solitary (Jolles *et al.*, 2016). This emphasises the dynamic nature of social interactions and that individuals likely do not respond in the same manner to different social environments (Taborsky & Oliveira, 2012; Araya-Ajoy *et al.*, 2015, 2020). Moreover, in our study about 13% of the variation in scrounging behaviour was attributable to variation among trials. This is likely a result of the fact that scrounging cannot occur when no wells have been produced within a trial, as other among trial differences such as trial order have been accounted for in the models. This shows how the immediate composition of phenotypes within the social environment can affect the expression of social behaviours.

We found small IIEs at the focal individual level (R = 0.013 & 0.029) and larger IIEs due to both social partners (R = 0.026 & 0.058) in producing and scrounging behaviour respectively. This means that a small portion of the variation in producing and scrounging behaviour is attributable to whom a focal individual interacts with. Typically, the amount of variation explained by indirect genetic effects is relatively low, and the average effect size is 6% for behavioural traits (Santostefano *et al.*, 2024). Since the IIEs consist of both additive genetic variance and permanent environment effects (Han *et al.*, 2018), IGEs in producing and scrounger behaviour will necessarily be smaller than our IIE estimates. The strength of indirect effects varies across different types of behaviour. For instance, aggressive behaviours are reciprocal which provides feedback loops that are often asymmetrical (i.e. winning a contest makes the other lose the contest), and therefore often have strong indirect effects (Wilson *et al.*, 2009, 2011; McGlothlin *et al.*, 2010; Santostefano *et al.*, 2016), which is likely why scrounging has a greater IIE than producing. The degree to which an individual produces or scrounges should depend upon the tactic chosen by its social partner(s) on average, as predicted by negative frequency-dependence (Giraldeau & Beauchamp, 1999; Giraldeau & Caraco, 2000; Giraldeau & Dubois, 2008). Our findings imply, however, that variation in producing and scrounging is not so much affected by social partners. Indicating that individuals may primarily be driven by variation in their energetic state, because the pay-offs for producing and scrounging vary based on energetic demands and body condition (Barta & Giraldeau, 2000). For example, captive house sparrows with poorer energy reserves due to overnight wind exposure have been shown to scrounge more during the very first foraging interactions of the day (Lendvai *et al.*, 2004).

An alternative explanation for our results might instead be that individual sparrows were responding to the total levels of producing and scrounging within a specific trial, rather than to the average behaviour of any particular social partner. This would seem sensible because individuals were not very consistent in their producing and scrounging behaviour, and individuals varied greatly among trials. This would suggest that individuals were 'socially responsive' to their immediate social environment (Wolf *et al.*, 2008; Dingemanse & Araya-Ajoy, 2015; Araya-Ajoy *et al.*, 2020), and plastically adjusted their social foraging tactic-use accordingly to some conditional ESSs, but irrespective of which individual was doing the producing or scrounging. The variance partitioning approach used in this study does not capture this social responsiveness, because plastic responses to immediate social partner' producing and scrounging in the social environment are not included here as they would be in a trait-based model (Moore *et al.*, 1997). In such models, any individual variation in plasticity would thus be captured as residual variation (Martin *et al.*, 2011). In order to further tease this apart, a random regression model is required where an individual's 'social responsiveness' to its social environment, and its 'social impact' on others are estimated in conjunction (de Groot *et al.*, 2023). In reality, the within individual variation in social phenotypes likely consists of a mixture of social responsiveness, state-dependency, along with additional unexplained variation in the environment.

Temporal consistency in DIEs & IIEs

Contrary to our initial predictions, both the DIE and the IIE in producing and scrounging behaviour showed high cross-year repeatability or temporal consistency. This indicates that individuals produce and scrounge similarly, and elicit the same amount of behavioural change in their social partners across years. Aplin & Morand-Ferron (2017) also found that average producing and scrounging behaviour was repeatable across years with an intraclass correlation approach. Overall, this suggests that the average DIEs and IIEs of individuals are consistent over time, but that individuals are highly plastic in their producing and scrounging behaviour between trials. Even though the (long-term) repeatability of the DIEs and IIEs presented here are not very high, the fact that these individual effects are conserved across time may suggest that there are certain 'types' of individuals with differential impact on others, similar to strategies within game-theory (Maynard-Smith, 1984; McNamara & Leimar, 2020). For instance, some individuals may consistently elicit higher or lower trait values in their social partners, whereas some individuals may have no impact at all. This is significant, because certain individuals may thus have disproportionate effects on the amount of heritable variation in the population (Araya-Ajoy *et al.*, 2020), and could be part of an individual's socially evolved strategy to play the producer-scrounger game.

Producer-scrounger theory and indirect effects

We found that producing and scrounging behaviour correlated negatively (r = -0.754), which has also been found by various other studies (Barnard & Sibly, 1981; Giraldeau *et al.*, 1994; Mottley & Giraldeau, 2000; Beauchamp, 2001), and is often an assumption in theoretical models (Barnard & Sibly, 1981; Giraldeau & Caraco, 2000; Giraldeau & Dubois, 2008). This indicates that individuals primarily opt for a purer producer-scrounger strategy. Moreover, the within-individual correlation between producing and scrounging behaviour was negative (r = -0.396), which further reinforces that individuals tend to opt for a particular tactic within a trial. However, because this relationship was not strongly negative this could also indicate that in many instances individuals opt for mixed or conditional strategies. We found that individuals that have a higher propensity to produce elicit more scrounging, but less producing in others, and *vice versa* for individuals that have a higher propensity to scrounge. Conversely, individuals that elicited more scrounging elicited less producing in others, reinforcing the idea that there are 'types' of individuals that vary in how much behaviour they elicit in others across traits.

Generally, our findings are in line with the negative frequency-dependence in producing-scrounging models at the population level, because more producing facilitates increased scrounging and increased scrounging increases the relative pay-off of producing, yielding the ESS (Giraldeau & Beauchamp, 1999; Giraldeau & Caraco, 2000). However, producer-scrounger game theory is derived at the population level for fitness consequences, and not at the trial-level with the amount of producing or scrounging events as is presented in this study, making it difficult to fully equate the two. Classic producer-scrounger models assume that individuals either adopt a deterministic pure, a probabilistic mixed strategy, or conditional plastic strategy (Caraco & Giraldea, 1991; Vickery *et al.*, 1991; Giraldeau & Beauchamp, 1999). Here, we show that producer-scrounger strategies are shaped by among-individual variation that contributes to the average tactic use, with IIEs that elicit behavioural change in others and within-individual variation that determines conditional strategy use. This suggests a more complex multivariate approach to tactic-use in house sparrows, which is not yet fully embedded into current game-theory. Our findings can thus be seen as further empirical information for future theoretical models of frequency-dependent behaviour that include quantitative genetic mechanisms (McGlothlin *et al.*, 2022).

Consequences of IIEs in producing and scrounging behaviour

As described above, indirect effects can have profound effects on the expressed phenotypic variation upon which selection can act, providing a potential explanation for slower or more rapid evolution of social traits than predicted by classic theory (Moore *et al.*, 1997; Wolf *et al.*, 1999; Bijma *et al.*, 2007b; McGlothlin *et al.*, 2010). The amount of variation explained by the IIEs in this study may seem marginal, but we showed that the total social phenotypic effect ($P\tau^2$) was 50% lower compared to the repeatability of the DIEs. Similar to repeatability, this would theoretically set the upper limit for heritability for traits with indirect effects. This suggests that IIEs in our system probably decrease the potential heritable variation as compared to assessments of only repeatability or heritability using direct effects of the phenotype (Bijma *et al.*, 2007a; b). Because the DIEs and IIEs in our birds exhibited high temporal consistency, these effects of IIEs in reducing any phenotypic variation are probably conserved across time.

Furthermore, we present a tight covariance structure between DIEs and IIEs in producing and scrounging behaviour. Phenotypic correlations explain 75% of the variance in genetic correlations in various behavioural traits, and thus seem to provide a reliable estimate of the sign and magnitude of the genetic relationship (Dochtermann, 2011). At either the phenotypic or at the genetic level, this tight covariance structure suggests limited autonomy for these phenotypes to evolve independently (Hansen & Houle, 2008). This is also observed in other behavioural syndromes (Dochtermann & Dingemanse, 2013), and may imply a coordinated social foraging behavioural syndrome. This suggests major evolutionary constraints for how the population mean phenotypic response will evolve in these populations due to selection. Together with the constraining effects on the phenotypic variation in producing and scrounging behaviour due to indirect effects, this suggests limited evolutionary change even under directional selection in this system, leading to potential evolutionary stasis (Wolf *et al.*, 1999; Bijma *et al.*, 2007b; McGlothlin *et al.*, 2010; Santostefano *et al.*, 2017). Ultimately, this tight covariance structure, and persistent constraining effects on the phenotypic variation due to indirect effects, could provide a potential explanation and mechanism for the existence of a phenotypic equilibrium or ESS in sparrow social foraging behaviour.

In conclusion, this study provides evidence for direct and indirect individual effects in the frequency-dependent producer-scrounger game. The DIEs and IIEs showed high temporal consistency, but showed modest and low (long-term) repeatability. Individuals opted for purer producer-scrounger tactics, but were highly plastic in their tactics use across trials. The DIEs and IIEs covaried strongly across producing and scrounging behaviour and imply constraint on evolutionary trajectories. Our findings also indicate the existence of individuals that varied in their social impact on others across traits. The indirect effects decreased the phenotypic variation for both behaviours and illustrate that indirect effects can slow down the rate of evolution. Together the reduced phenotypic variation and trait covariance provide evidence for potential evolutionary stasis that can maintain the equilibrium state at the ESS. Our findings underline the importance of indirect effects and multivariate approaches in light of social evolution, which will allow for better models and understanding of the maintenance of phenotypic variation.

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Ethics statement

All experimental procedures conformed with the ethical guidelines concerning the capture and use of animals in research and were approved by the Norwegian Food Safety Authority (FOTS ID 29007) and the Norwegian Bird Ringing Centre.

Data & code availability.

Data and code for analyses are available at: https://github.com/C-dG/DIE_IIE_cov_PS

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Supplemental material

Supplemental text 1: Univariate models

We fitted Focal ID and social partner IDs as random effects to partition the direct individual effect (DIE) and indirect individual effect (IIE), and their covariance. Variance due to social partner IDs (IIE) was constrained to be equal, since the assignment of social partner IDs was arbitrary. To account for our study design, we fitted (triadic) trial day (1 – 2), and individual trial order (1 – 10), as fixed effects, and TrialID (n = 1997), and GroupID (n = 53) as random effects. Trial order and trial day were mean centred such that the intercept was estimated for the average trial for an individual. We fitted interactions between trial day and trial order to account for habituation effects during the trials. For the 2022 models, we fitted an additional binary fixed effect for individuals that were included for the BMR measurements (n = 127) during the first habituation day. For the 2023 models, we fitted an additional binary fixed effect for individuals that participated in the full group trials before starting the triadic trials (n = 36) to account for habituation effects. Individuals that participated in full group trials prior to triadic trials produced and scrounged more. Therefore, we fitted an additional three-way interaction between trial day, trial order and group trial before to account for differences in habituation at these three levels. For the full dataset, we also fitted year (2022 – 2023) as a fixed effect. Individuals that partook in the BMR measurements prior to habituation did not behave differently, and this parameter was therefore dropped from the full model. The full model provided similar patterns compared to the split models for each year and trial day (see Suppl. Table 2 & 3).

Supplemental text 2: Repeatability equations

$$(long - term)\ Repeatability = \frac{\sigma^2 DIE}{\sigma^2 Total}$$

Equation 1

The variance standardised repeatability is calculated by dividing the variance of a given parameter, in this case the variance for the direct individual effect (DIE), by the total variance, which is the sum of all the variances and the residual variance estimated by the model. For the total variance we summed the product of the IIE multiplied by 2, because a focal individual's phenotype is determined by both its social partners IIEs.

$$Short - term\ repeatability = \frac{\sigma^2 DIE + \sigma^2 Series\ FocalID, Year}{\sigma^2 Total}$$

Equation 2

The short-term repeatability is calculated by summing the variance of the parameter of interest (i.e. the product for the long-term repeatability) and the variance of the series parameter. The series parameter consists of the index of the focalID and the year of the observation (e.g. Focal_ID152_year2022). For IIEs the series parameter consists of the opponent IDs instead of the focal ID.

$$Cross - year\ repeatability = \frac{\sigma^2 DIE}{\sigma^2 DIE + \sigma 2 Series\ FocalID, Year}$$

Equation 3

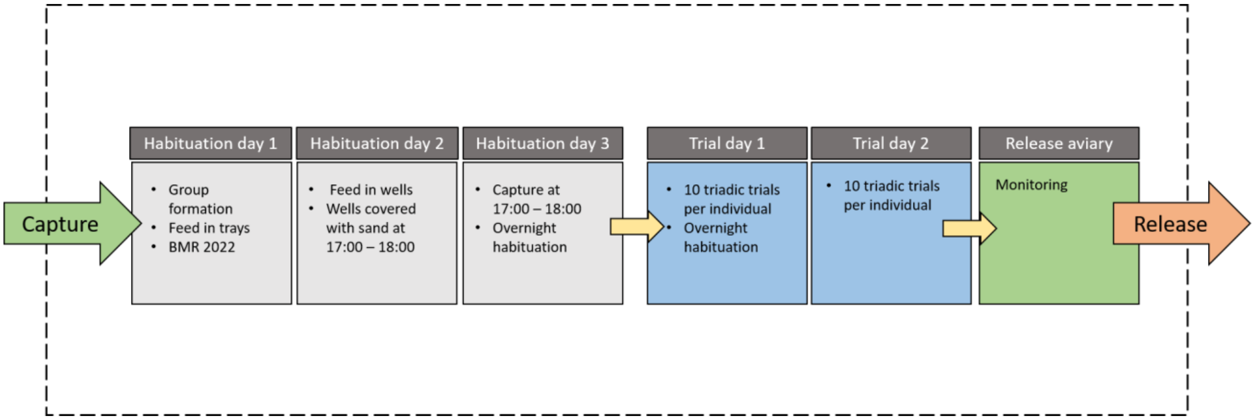
The cross-year or average repeatability is calculated by dividing the long-term repeatability numerator by the short-term repeatability numerator and represents the average repeatability of the trait across the measurements. In this specific scenario we measured this across two years and thus represents whether individuals are consistent across the two years. Note that the equation to estimate cross-year repeatability does not include any residual variance, but estimates how the short and long-term repeatability relate to one another. For further reading see: Araya-Ajoy YG, Mathot KJ, Dingemanse NJ. 2015 An approach to estimate short-term, long-term and reaction norm repeatability. Methods in Ecology and Evolution 6, 1462–1473. (doi:10.1111/2041-210X.12430).

Supplemental text 3: The total social phenotypic effect

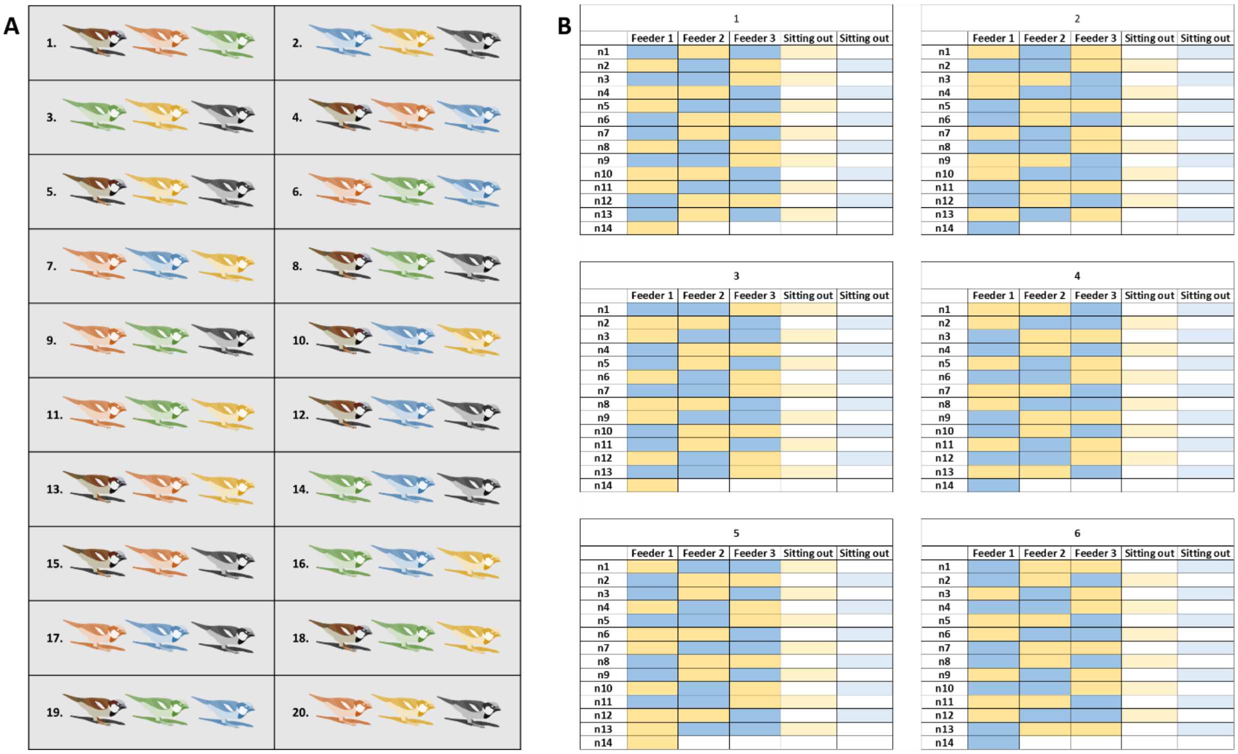
$$P\tau^2 = \frac{\sigma^2 DIE + \sigma DIE, IIE\ 2(n-1)\ + \sigma^2 IIE\ (n-1)}{\sigma^2 P}$$

Equation 4

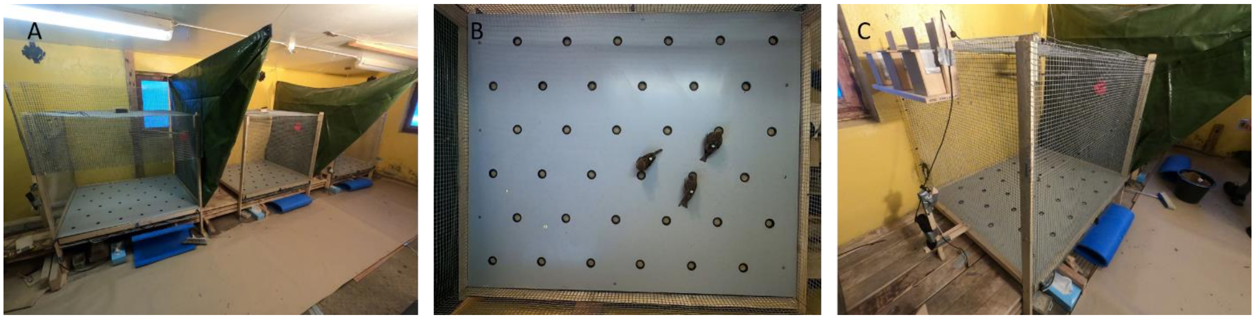
The total social phenotypic effect ($P\tau^2$) was calculated by dividing the sum of the DIE variance, the covariance between the DIE and IIE, and the IIE variance, divided by the total phenotypic variation. This yields a fraction of variance explained by $P\tau^2$ compared to the total phenotypic variation, and would theoretically set the upper bound for the total heritable variation in a trait due to interacting phenotypes (τ^2). To account for the number of interacting social partners, the covariance between the DIE and the IIE and the IIE variance are multiplied by n-1, which is 3 minus 1 in our case. For further reading see: Bijma P, Muir WM, Van Arendonk JAM. 2007 Multilevel selection 1: Quantitative genetics of inheritance and response to selection. Genetics 175, 277–288. (doi:10.1534/genetics.106.062711).



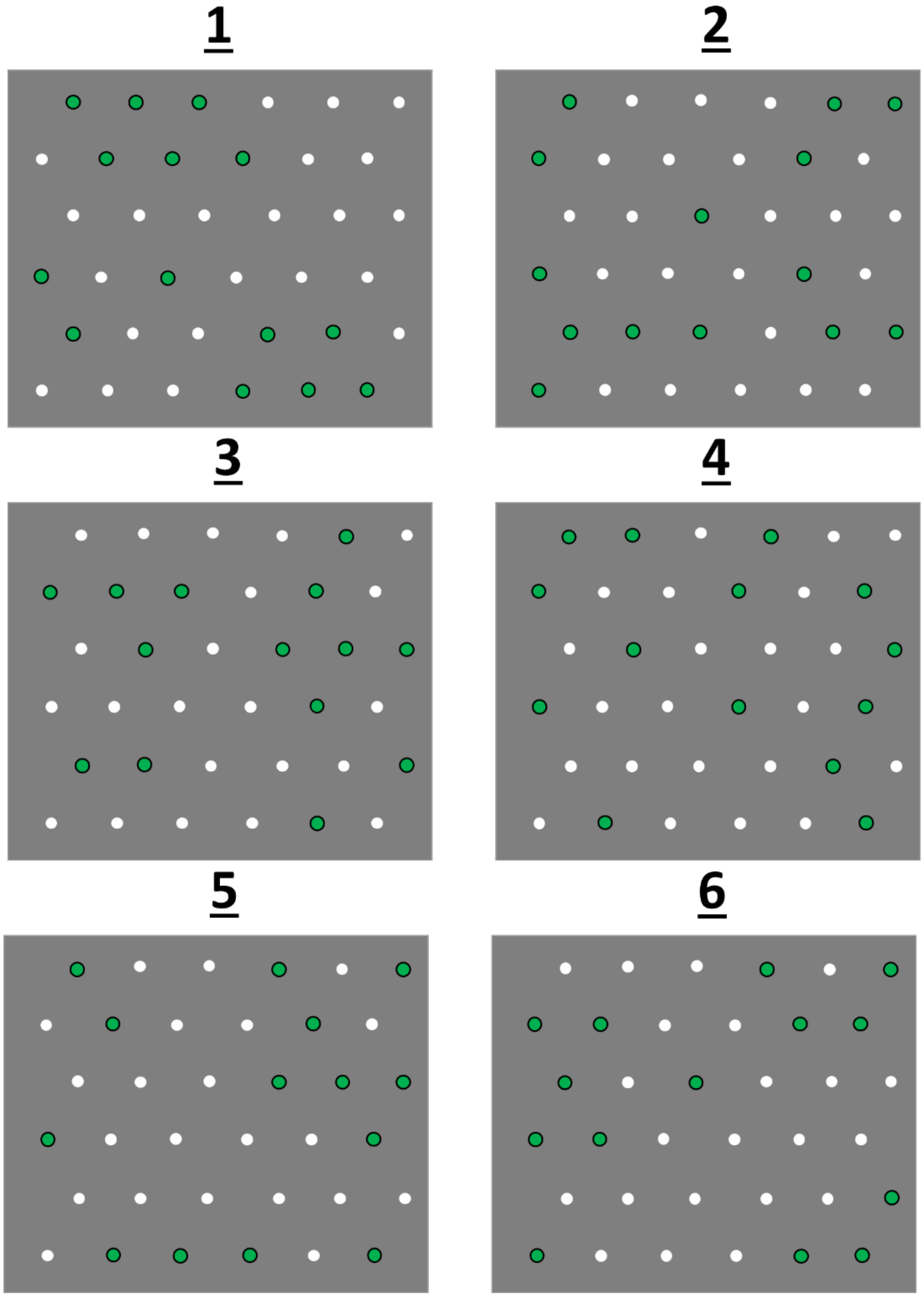
Supplemental Figure 1: Schematic overview of the steps in the habituation process, experiments and subsequent release.



Supplemental Figure 2: A schematic overview of: (A) the 20 possible combinations used during the experiments to manipulate the social phenotypes to which individuals were exposed to. (B) The 6 different patterns to which triadic combinations can be assigned to the 3 different feeders, the different colours represent the different groups (A – F, G – K). Sitting out individuals did not play a trial but remained in their individual nestbox during a running trial to prevent satiation and maintain motivation



Supplemental Figure 3: Photos of the experimental setup: (A) The 3 checkerboard feeders in caged mesh wire structures in the experimental room. (B) A top down view of the checkerboard feeder during a trial. (C) A side view of a checkerboard feeder with the three individual nestboxes on the left side of the cage construction. A pulley mechanism made with fishing wire was used to open and close the nestbox that was closest to the wall from a distance so birds could more easily be flushed into a nestbox.

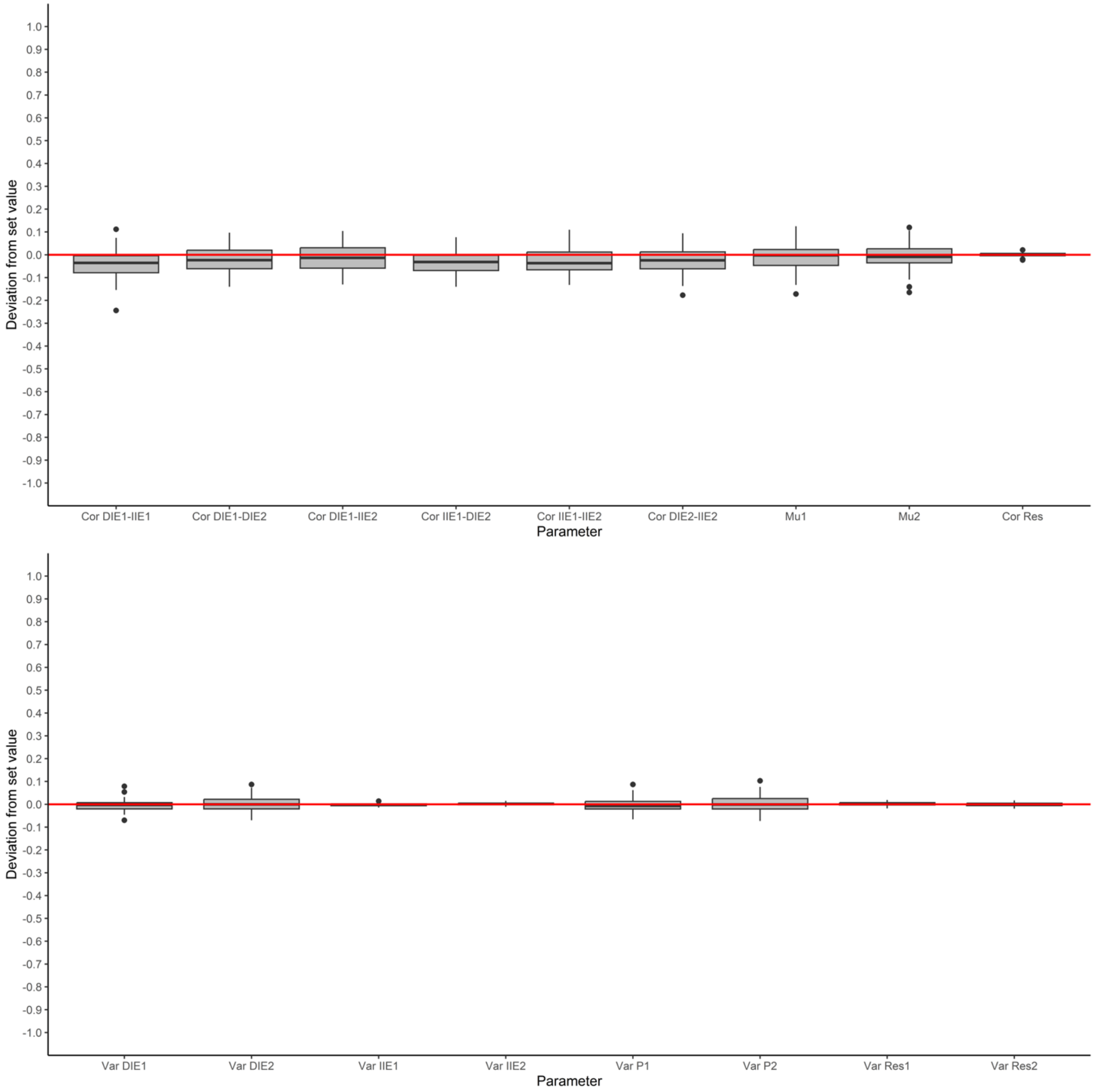


Supplemental Figure 4: The 6 randomised patterns of baited wells, the green circles represent wells that are baited with millet seeds and the open circles represent wells filled with only sand. Which order was used to fill a checkerboard feeder for that particular trial was based on a dice roll (1 – 6), where the number of eyes corresponds with the pattern that was used. A second dice roll determined whether the orientation of the pattern with which the feeder was filled non-rotated (1 -3) or rotated by 180 degrees (4- 6).

Supplemental Table 1: The ethogram used in BORIS to score the videos, during video analysis. State events have a duration (s) with a start and stop time, whereas point events are counts with a timestamp.

Behaviour	Event type	Category	Description
Search/produce	State event	Foraging	Sieving through sand/beak is visibly in the well.
Join/scrounge	State event	Foraging	Joining a well or feeding from seeds around a well (<2cm) that another individual is sampling from. Includes attempts at joining. Also includes the recipient and outcome of the behaviour (whether 1) the focal individual leaves, 2) the social partner leaves, 3) both leave, 4) both stay , or 5) it is a latent join). Score as latent join when resident left shortly (no longer than 3 seconds) before focal arrived.
Secondary find	State event	Foraging	Same criteria as search, but the well has clear visual cues for seeds.
Feed	Point event	Foraging	Consuming one seed either from board or a well.
Revisit	State event	Foraging	Leaving the well and returning to the same well within less than 10 seconds, without visiting another well or stopping feeding for longer than 5 seconds, but staying at the same well. Includes which behaviour was resumed (Search/Join/Secondary search).
Attack	Point event	Aggression	Short peck or attack launched and not directly reciprocated.
Aggression	Point event	Aggression	Fighting/directly reciprocated attack initiated by the focal individual. Includes the recipient, outcome (whether 1) the focal individual leaves, 2) the social partner leaves, 3) both leave, 4) both stay), and duration (any 0.5 second interval between 0 and 5 seconds, or longer than 5 seconds) of the behaviour.
Display	Point event	Aggression	Wing display or flapping. Count each display or flap.
Board	State event	Methodological	Standing on the board.

Reference tag	Point event	Methodological	The moment the reference tag is tapped on the feeder.
Release	Point event	Methodological	The moment the first bird is released, which indicates the start time of the 15-minute trial.



Supplemental Figure 5: Boxplots based on the estimated (upper panel) correlations and (lower panel) variances by the bivariate stan model based on 50 simulated datasets with the same structure as the data used in the analyses. The data represented here is based on the median estimate minus the set value for the parameter. Models were fitted with one chain, 2000 warmup iterations and 3000 sampling iterations, similar to the iterations used in the final models. The variances were estimated with little bias, but some of the correlations show some, but overall small bias.

Supplemental Table 2: Posterior medians with the 95% credible intervals between parentheses for producing behaviour for models split per year and trial day, for the direct individual effect (DIE) and indirect individual effect (IIE).

Variable	*2022*	*2022 day1*	*2022 day2*	*2023*	*2023 day1*	*2023 day2*	*2022/2023*
Fixed effects	*β (95% CI)*	*β (95% CI)*	*β (95% CI)*	*β (95% CI)*	*β (95% CI)*	*β (95% CI)*	*β (95% CI)*
Intercept producing	*1.464 (1.296 ; 1.636)*	*1.411 (1.215 ; 1.612)*	*1.498 (1.303 ; 1.692)*	*1.489 (1.375 ; 1.601)*	*1.506 (1.385 ; 1.628)*	*1.486 (1.366 ; 1.607)*	*1.545 (1.469 ; 1.623)*
Year	-	-	-	-	-	-	*-0.116 (-0.246 ; 0.016)*
BMR	*0.166 (-0.041 ; 0.367)*	*0.183 (-0.051 ; 0.415)*	*0.169 (-0.060 ; 0.399)*	-	-	-	-
Trial order	*0.033 (0.018 ; 0.048)*	*0.035 (0.012 ; 0.057)*	*0.030 (0.011 ; 0.048)*	*0.026 (0.008 ; 0.044)*	*0.048 (0.020 ; 0.077)*	*0.005 (-0.017 ; 0.028)*	*0.030 (0.018 ; 0.041)*
Trial day	*0.109 (0.026 ; 0.193)*	-	-	*-0.012 (-0.114 ; 0.089)*	-	-	*0.063 (-0.003 ; 0.128)*
Group trial before	-	-	-	*-0.205 (-0.422 ; 0.008)*	*-0.169 (-0.399 ; 0.064)*	*-0.261 (-0.495 ; -0.028)*	*-0.201 (-0.415 ; 0.005)*
*Trial day * Group trial before*	-	-	-	*-0.097 (-0.288 ; 0.097)*	-	-	*-0.173 (-0.355 ; 0.008)*
*Trial order * Group trial before*	-	-	-	*-0.016 (-0.050 ; 0.017)*	*-0.031 (-0.081 ; 0.019)*	*0.000 (-0.045 ; 0.044)*	*-0.018 (-0.050 ; 0.013)*
*Trial day * Trial order*	*-0.005 (-0.027 ; 0.019)*	-	-	*-0.038 (-0.074 ; -0.001)*	-	-	*-0.018 (-0.041 ; 0.004)*
*Trial day * Trial order * Group trial before*	-	-	-	*0.025 (-0.042 ; 0.093)*	-	-	*0.005 (-0.056 ; 0.068)*
Random effects	*σ² (95% CI)*	*σ² (95% CI)*	*σ² (95% CI)*	*σ² (95% CI)*	*σ² (95% CI)*	*σ² (95% CI)*	*σ² (95% CI)*
DIE	*0.420 (0.323 ; 0.547)*	*0.442 (0.319 ; 0.608)*	*0.441 (0.329 ; 0.589)*	*0.273 (0.196 ; 0.380)*	*0.274 (0.178 ; 0.406)*	*0.295 (0.204 ; 0.422)*	*0.336 (0.269 ; 0.419)*
IIE	*0.020 (0.010 ; 0.035)*	*0.034 (0.014 ; 0.064)*	*0.019 (0.006 ; 0.038)*	*0.014 (0.004 ; 0.030)*	*0.015 (0.001 ; 0.041)*	*0.019 (0.004 ; 0.048)*	*0.019 (0.011 ; 0.030)*
Group	*0.003 (0.000 ; 0.025)*	*0.005 (0.000 ; 0.047)*	*0.003 (0.000 ; 0.036)*	*0.018 (0.000 ; 0.074)*	*0.010 (0.000 ; 0.067)*	*0.011 (0.000 ; 0.071)*	*0.028 (0.009 ; 0.059)*
Trial	*0.000 (0.000 ; 0.007)*	*0.002 (0.000 ; 0.016)*	*0.002 (0.000 ; 0.016)*	*0.000 (0.000 ; 0.007)*	*0.001 (0.000 ; 0.015)*	*0.001 (0.000 ; 0.015)*	*0.000 (0.000 ; 0.005)*
Residual variance	*1.214 (1.151 ; 1.283)*	*1.287 (1.186 ; 1.398)*	*1.074 (0.997 ; 1.163)*	*1.096 (1.032 ; 1.165)*	*1.157 (1.057 ; 1.271)*	*1.006 (0.924 ; 1.099)*	*1.175 (1.129 ; 1.223)*
Total variance	*1.663 (1.542 ; 1.805)*	*1.781 (1.623 ; 1.970)*	*1.546 (1.409 ; 1.715)*	*1.411 (1.309 ; 1.533)*	*1.468 (1.334 ; 1.631)*	*1.347 (1.225 ; 1.493)*	*1.561 (1.478 ; 1.659)*
Covariance	*σ (95% CI)*	*σ (95% CI)*	*σ (95% CI)*	*σ (95% CI)*	*σ (95% CI)*	*σ (95% CI)*	*σ (95% CI)*
DIE-IIE	*-0.063 (-0.092 ; -0.041)*	*-0.080 (-0.122 ; -0.047)*	*-0.063 (-0.098 ; -0.035)*	*-0.043 (-0.067 ; -0.023)*	*-0.040 (-0.075 ; -0.011)*	*-0.046 (-0.080 ; -0.018)*	*-0.056 (-0.075 ; -0.040)*
Repeatability	*R (95% CI)*	*R (95% CI)*	*R (95% CI)*	*R (95% CI)*	*R (95% CI)*	*R (95% CI)*	*R (95% CI)*
DIE	*0.253 (0.206 ; 0.306)*	*0.249 (0.190 ; 0.315)*	*0.285 (0.226 ; 0.351)*	*0.194 (0.145 ; 0.254)*	*0.187 (0.126 ; 0.258)*	*0.220 (0.159 ; 0.292)*	*0.215 (0.179 ; 0.256)*
IIE	*0.012 (0.006 ; 0.021)*	*0.019 (0.008 ; 0.036)*	*0.012 (0.004 ; 0.024)*	*0.010 (0.003 ; 0.021)*	*0.010 (0.001 ; 0.028)*	*0.015 (0.003 ; 0.036)*	*0.012 (0.007 ; 0.019)*
Group	*0.002 (0.000 ; 0.015)*	*0.003 (0.000 ; 0.026)*	*0.002 (0.000 ; 0.023)*	*0.014 (0.000 ; 0.051)*	*0.007 (0.000 ; 0.045)*	*0.008 (0.000 ; 0.052)*	*0.018 (0.006 ; 0.038)*
Trial	*0.000 (0.000 ; 0.004)*	*0.001 (0.000 ; 0.009)*	*0.001 (0.000 ; 0.010)*	*0.000 (0.000 ; 0.005)*	*0.001 (0.000 ; 0.010)*	*0.001 (0.000 ; 0.011)*	*0.000 (0.000 ; 0.002)*
Residual	*0.731 (0.676 ; 0.780)*	*0.724 (0.656 ; 0.784)*	*0.696 (0.630 ; 0.755)*	*0.778 (0.721 ; 0.825)*	*0.789 (0.720 ; 0.848)*	*0.749 (0.680 ; 0.808)*	*0.753 (0.711 ; 0.790)*
Correlations	*r (95% CI)*	*r (95% CI)*	*r (95% CI)*	*r (95% CI)*	*r (95% CI)*	*r (95% CI)*	*r (95% CI)*
DIE-IIE	*-0.927 (-0.997 ; -0.715)*	*-0.905 (-0.996 ; -0.647)*	*-0.907 (-0.997 ; -0.641)*	*-0.851 (-0.993 ; -0.508)*	*-0.820 (-0.992 ; -0.350)*	*-0.746 (-0.986 ; -0.330)*	*-0.909 (-0.995 ; -0.708)*

Supplemental Table 3: Posterior medians with the 95% credible intervals between parentheses for scrounging behaviour for models split per year and trial day for the direct individual effect (DIE) and indirect individual effect (IIE).

Variable	*2022*	*2022 day1*	*2022 day2*	*2023*	*2023 day1*	*2023 day2*	*2022/2023*
Fixed effects	*β (95% CI)*	*β (95% CI)*	*β (95% CI)*	*β (95% CI)*	*β (95% CI)*	*β (95% CI)*	*β (95% CI)*
Intercept scrounging	*0.709 (0.594 ; 0.823)*	*0.766 (0.612 ; 0.917)*	*0.655 (0.539 ; 0.774)*	*0.596 (0.532 ; 0.661)*	*0.581 (0.500 ; 0.660)*	*0.609 (0.528 ; 0.690)*	*0.644 (0.599 ; 0.687)*
Year	-	-	-	-	-	-	*-0.079 (-0.155 ; -0.006)*
BMR	*-0.034 (-0.161 ; 0.099)*	*-0.030 (-0.201 ; 0.142)*	*-0.036 (-0.174 ; 0.102)*	-	-	-	-
Trial order	*0.017 (0.007 ; 0.027)*	*0.028 (0.012 ; 0.044)*	*0.006 (-0.006 ; 0.019)*	*0.021 (0.009 ; 0.034)*	*0.032 (0.014 ; 0.050)*	*0.010 (-0.005 ; 0.026)*	*0.019 (0.011 ; 0.027)*
Trial day	*-0.110 (-0.167 ; -0.055)*	-	-	*0.040 (-0.030 ; 0.110)*	-	-	*-0.052 (-0.094 ; -0.010)*
Group trial before	-	-	-	*0.109 (-0.017 ; 0.234)*	*0.144 (-0.008 ; 0.298)*	*0.075 (-0.083 ; 0.230)*	*0.098 (-0.022 ; 0.219)*
*Trial day * Group trial before*	-	-	-	*-0.085 (-0.218 ; 0.047)*	-	-	*0.012 (-0.112 ; 0.134)*
*Trial order * Group trial before*	-	-	-	*-0.013 (-0.036 ; 0.009)*	*-0.039 (-0.072 ; -0.007)*	*0.014 (-0.016 ; 0.045)*	*-0.011 (-0.032 ; 0.010)*
*Trial day * Trial order*	*-0.026 (-0.049 ; -0.002)*	-	-	*-0.023 (-0.048 ; 0.002)*	-	-	*-0.022 (-0.038 ; -0.006)*
*Trial day * Trial order * Group trial before*	-	-	-	*0.053 (0.008 ; 0.100)*	-	-	*0.052 (0.010 ; 0.095)*
Random effects	*σ² (95% CI)*	*σ² (95% CI)*	*σ² (95% CI)*	*σ² (95% CI)*	*σ² (95% CI)*	*σ² (95% CI)*	*σ² (95% CI)*
DIE	*0.121 (0.089 ; 0.166)*	*0.124 (0.079 ; 0.184)*	*0.144 (0.103 ; 0.199)*	*0.080 (0.054 ; 0.115)*	*0.092 (0.056 ; 0.141)*	*0.116 (0.077 ; 0.169)*	*0.107 (0.083 ; 0.137)*
IIE	*0.029 (0.019 ; 0.043)*	*0.036 (0.019 ; 0.062)*	*0.021 (0.011 ; 0.037)*	*0.010 (0.004 ; 0.020)*	*0.018 (0.006 ; 0.035)*	*0.006 (0.001 ; 0.017)*	*0.021 (0.014 ; 0.029)*
Group	*0.012 (0.000 ; 0.034)*	*0.021 (0.000 ; 0.059)*	*0.004 (0.000 ; 0.023)*	*0.006 (0.000 ; 0.024)*	*0.006 (0.000 ; 0.030)*	*0.006 (0.000 ; 0.032)*	*0.005 (0.000 ; 0.016)*
Trial	*0.001 (0.000 ; 0.016)*	*0.003 (0.000 ; 0.028)*	*0.003 (0.000 ; 0.021)*	*0.001 (0.000 ; 0.015)*	*0.006 (0.000 ; 0.037)*	*0.001 (0.000 ; 0.015)*	*0.001 (0.000 ; 0.008)*
Residual	*0.547 (0.518 ; 0.579)*	*0.602 (0.553 ; 0.659)*	*0.466 (0.430 ; 0.506)*	*0.500 (0.470 ; 0.532)*	*0.459 (0.414 ; 0.508)*	*0.484 (0.444 ; 0.528)*	*0.532 (0.510 ; 0.554)*
Total	*0.715 (0.668 ; 0.773)*	*0.795 (0.729 ; 0.876)*	*0.644 (0.588 ; 0.709)*	*0.602 (0.563 ; 0.648)*	*0.587 (0.534 ; 0.650)*	*0.619 (0.565 ; 0.684)*	*0.666 (0.633 ; 0.705)*
Covariance	*σ (95% CI)*	*σ (95% CI)*	*σ (95% CI)*	*σ (95% CI)*	*σ (95% CI)*	*σ (95% CI)*	*σ (95% CI)*
DIE-IIE	*-0.056 (-0.078 ; -0.039)*	*-0.056 (-0.084 ; -0.034)*	*-0.055 (-0.080 ; -0.037)*	*-0.028 (-0.044 ; -0.016)*	*-0.036 (-0.061 ; -0.016)*	*-0.023 (-0.043 ; -0.004)*	*-0.042 (-0.056 ; -0.031)*
Repeatability	*R (95% CI)*	*R (95% CI)*	*R (95% CI)*	*R (95% CI)*	*R (95% CI)*	*R (95% CI)*	*R (95% CI)*
DIE	*0.169 (0.129 ; 0.221)*	*0.157 (0.104 ; 0.220)*	*0.223 (0.168 ; 0.288)*	*0.133 (0.093 ; 0.183)*	*0.156 (0.097 ; 0.225)*	*0.188 (0.130 ; 0.256)*	*0.160 (0.129 ; 0.198)*
IIE	*0.040 (0.026 ; 0.060)*	*0.046 (0.024 ; 0.077)*	*0.033 (0.018 ; 0.056)*	*0.017 (0.007 ; 0.033)*	*0.030 (0.010 ; 0.059)*	*0.009 (0.001 ; 0.027)*	*0.031 (0.021 ; 0.043)*
Group	*0.017 (0.000 ; 0.047)*	*0.027 (0.000 ; 0.073)*	*0.006 (0.000 ; 0.034)*	*0.011 (0.000 ; 0.039)*	*0.010 (0.000 ; 0.050)*	*0.009 (0.000 ; 0.050)*	*0.007 (0.000 ; 0.025)*
Trial	*0.002 (0.000 ; 0.022)*	*0.004 (0.000 ; 0.035)*	*0.004 (0.000 ; 0.032)*	*0.003 (0.000 ; 0.024)*	*0.010 (0.000 ; 0.063)*	*0.002 (0.000 ; 0.024)*	*0.001 (0.000 ; 0.012)*
Residual	*0.767 (0.714 ; 0.811)*	*0.759 (0.692 ; 0.817)*	*0.726 (0.661 ; 0.782)*	*0.831 (0.781 ; 0.873)*	*0.782 (0.705 ; 0.848)*	*0.783 (0.716 ; 0.840)*	*0.798 (0.759 ; 0.831)*
Correlations	*r (95% CI)*	*r (95% CI)*	*r (95% CI)*	*r (95% CI)*	*r (95% CI)*	*r (95% CI)*	*r (95% CI)*
DIE-IIE	*-0.825 (-0.981 ; -0.620)*	*-0.790 (-0.987 ; -0.465)*	*-0.835 (-0.989 ; -0.596)*	*-0.793 (-0.988 ; -0.453)*	*-0.736 (-0.982 ; -0.353)*	*-0.739 (-0.988 ; -0.215)*	*-0.748 (-0.914 ; -0.583)*

Supplemental Table 4: Posterior medians with the 95% credible intervals between parentheses for producing and scrounging behaviour for cross-year repeatability models for the direct individual effect (DIE) and indirect individual effect (IIE).

Variables	*Producing*	*Scrounging*
Fixed effects	*β (95% CI)*	*β (95% CI)*
Intercept	*1.544 (1.474 ; 1.615)*	*0.644 (0.599 ; 0.687)*
Year	*-0.110 (-0.231 ; 0.015)*	*-0.080 (-0.159 ; -0.004)*
Trial order	*0.030 (0.019 ; 0.042)*	*0.019 (0.011 ; 0.027)*
Trial day	*0.064 (-0.001 ; 0.128)*	*-0.053 (-0.096 ; -0.009)*
Group trial before	*-0.208 (-0.401 ; -0.020)*	*0.104 (-0.018 ; 0.231)*

Trial day * Group trial before	-0.170 (-0.354 ; 0.011)	0.010 (-0.114 ; 0.133)
Trial day * Trial order	-0.018 (-0.041 ; 0.004)	-0.022 (-0.038 ; -0.007)
Trial order * Group trial before	-0.019 (-0.051 ; 0.011)	-0.011 (-0.032 ; 0.010)
Trial day * Trial order * Group trial before	0.006 (-0.056 ; 0.069)	0.053 (0.010 ; 0.096)
Random effects	σ² (95% CI)	σ² (95% CI)
DIE	0.242 (0.135 ; 0.343)	0.083 (0.048 ; 0.118)
IIE	0.013 (0.003 ; 0.025)	0.012 (0.001 ; 0.023)
Trial	0.008 (0.000 ; 0.036)	0.004 (0.000 ; 0.015)
Group	0.000 (0.000 ; 0.003)	0.001 (0.000 ; 0.009)
Series DIE	0.109 (0.047 ; 0.214)	0.022 (0.003 ; 0.053)
Series IIE	0.005 (0.000 ; 0.016)	0.008 (0.000 ; 0.021)
Residual	1.162 (1.115 ; 1.211)	0.527 (0.506 ; 0.549)
Total	1.564 (1.481 ; 1.664)	0.682 (0.647 ; 0.722)
Covariance	σ (95% CI)	σ (95% CI)
DIE-IIE	-0.038 (-0.060 ; -0.013)	-0.028 (-0.047 ; -0.005)
series DIE-IIE	-0.014 (-0.038 ; 0.000)	-0.012 (-0.033 ; 0.000)
Repeatability	R (95% CI)	R (95% CI)
DIE	0.155 (0.087 ; 0.211)	0.123 (0.071 ; 0.167)
IIE	0.008 (0.002 ; 0.016)	0.018 (0.002 ; 0.034)
Trial	0.000 (0.000 ; 0.002)	0.001 (0.000 ; 0.013)
Group	0.005 (0.000 ; 0.023)	0.006 (0.000 ; 0.022)
Series DIE	0.070 (0.030 ; 0.136)	0.032 (0.005 ; 0.078)
Series IIE	0.003 (0.000 ; 0.010)	0.011 (0.000 ; 0.030)
Residual	0.743 (0.701 ; 0.780)	0.774 (0.735 ; 0.809)
Cross-year rep DIE	0.693 (0.403 ; 0.866)	0.794 (0.495 ; 0.965)
Cross-year rep IIE	0.745 (0.179 ; 0.997)	0.633 (0.065 ; 0.985)
Correlations	r (95% CI)	r (95% CI)
DIE-IIE	-0.881 (-0.994 ; -0.561)	-0.742 (-0.970 ; -0.385)
series DIE-IIE	-0.814 (-0.993 ; 0.167)	-0.844 (-0.994 ; -0.081)

	Full	*Unadjusted*
Covariance	*σ (95% CI)*	*σ (95% CI)*
Trial	*0.039 (0.030 ; 0.049)*	*0.044 (0.033 ; 0.054)*
Group	*0.000 (-0.009 ; 0.008)*	*0.001 (-0.009 ; 0.011)*
Correlations	*r (95% CI)*	*r (95% CI)*
Trial	*0.981 (0.901 ; 0.999)*	*0.983 (0.907 ; 0.999)*
Group	*-0.098 (-0.920 ; 0.846)*	*0.075 (-0.831 ; 0.878)*

Supplemental Table 5: Posterior medians with 95% credible intervals (in parentheses) for the full and unadjusted bivariate models for covariance and correlation estimates for trial, group-level effects.