Dynamic strategic social learning in nest-building zebra finches and its generalisability

Alexis J. Breen[1,2,†], Tristan Eckersley[3], Andrés Camacho-Alpízar[3], Connor T. Lambert[3], Gopika Balasubramanian[3], Susan D. Healy[2], Richard McElreath[1,§] and Lauren M. Guillette[2,3,§]

[1]Department of Human Behavior, Ecology and Culture, Max Planck Institute for Evolutionary Anthropology; Leipzig 04103, Germany.

[2]School of Biology, University of St Andrews; St Andrews, Fife, KY16 9ST, United Kingdom.

[3]Department of Psychology, University of Alberta; Edmonton, Alberta, T6G 2R3, Canada.

[†]Present address: Department of Linguistic and Cultural Evolution, Max Planck Institute for Evolutionary Anthropology, Leipzig 04103, Germany

[§]Shared senior authors

[*]Correspondence: alexis_breen@eva.mpg.de; guillett@ualberta.ca

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Data accessibility. All data and code to reproduce the statistical analyses and figures are freely available at the GitHub repository: https://github.com/alexisbreen/Dynamic-nest-building.

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Abstract

Animals often balance asocial and social information strategically, adjusting when and from whom they copy based on context. Yet the cognition driving this dynamic—and its broader implications—remains poorly understood. Here, we show that nest-building zebra finches follow a *copy-if-dissatisfied* strategy, but only when social information aligns with recent experience: after observing a conspecific build a nest, males were more likely to choose the demonstrated 'social' material—particularly on their first choice—if they had previously used low-quality material. Using Bayesian cognitive modelling, we estimated how latent learning mechanisms underpinned males' material choices, identifying two asocial and two social governing parameters. These parameters provide the first formal evidence for the cognitive basis of birds' nest building. Forward simulations informed—but not prescripted—by these parameters approximated observed material-choice trajectories, supporting their causal role. Additional simulations targeting simplified real-world contexts showed that payoff structure—not (dis)satisfaction—drove social material choice, though higher rewards did not proportionally boost its use, offering preliminary insights into the mechanisms underlying material-use variation more broadly. Our study illustrates how computational modelling can robustly link behaviour to underlying learning mechanisms and probe the generalisability of animal cognition—a rarity in this field.

1 Introduction

Strategic social learning refers to a suite of decision rules individuals may use to determine when to rely on socially provided information, such as *copy-if-kin*, *copy-if-friends*, and *copy-if-dissatisfied* [1]. These strategies require balancing personal experience (asocial information) with public cues (social information), then updating that balance in light of outcomes. Striking this balance is complex: over-reliance on either source could be costly [2]. While behavioural evidence for such strategies is widespread across taxa (recent review: [3]), the cognitive mechanisms that enable this dynamic balancing—especially in non-human animals—remain largely 'blackboxed' [4].

By contrast, computational modelling in human studies has made significant progress in 'unblackboxing' the dynamic processes underlying strategic social learning [5], from the individual level to the crowd level [6, 7]. This analytical approach typically involves building a statistical model or models to infer cognition from behaviour—quantifying, for instance, the influence of asocial mechanisms like reinforcement learning and social mechanisms like conformity [8]. These mechanistic estimates can then be used in forward simulations, which predict agents' behaviour based on the inferred cognitive processes [9, 10]. When simulated behaviour aligns with observed data, the model is considered a good approximation of the underlying mechanisms [11, 12, 13]; when it does not, mismatches should prompt transparent reporting of limitations [14]. Such simulations also allow researchers to test how behaviour might change under new contexts, such as altered payoffs [14], to evaluate how well the model generalises beyond the original study [9, 10].

The growing recognition of computational modelling's explanatory power in non-human animal cognition [15] has likely contributed to its emerging application in studies of strategic social learning in these systems. To date, at least four studies—on tits [13], monkeys [16, 17], and chimpanzees [18]—have applied this framework (*sensu* [8]) to infer the roles of asocial and social learning in foraging behaviour. For example, tits were found to determine 'what to eat' primarily through reward-based individual updating and frequency-based conspecific copying, with these strategies supported by forward simulations [13]. Further such simulations manipulating agents' copying levels demonstrated that the moderate social conformity observed in real birds generally maximised foraging returns [13]

Nest building, like foraging, strongly impacts birds' fitness and may also favour strategic social learning [19, 20, 21, 22, 23]. Here, we examined strategic social learning in laboratory-housed, nest-building zebra finches—a species in which both asocial and social learning influence males' material choices [20, 24, 25, 26]. We asked: (i) do males use a *copy-if-dissatisfied* strategy? and (ii) does its use depend on the *type* of dissatisfaction? We induced dissatisfaction in two ways: (1) by having males build with flexible string—a low-quality material that requires greater investment to maximise reproductive success [27, 28]; or (2) by removing clutches during incubation—a manipulation known to influence later material choices [29, 30]. In one group, males built a partial nest using either stiff or flexible string. In another group, all males built with breeder-standard coconut fibre, but only half successfully reproduced. We then assessed each male's initial material preference (orange versus pink string), allowed them to observe a conspecific building with their non-preferred colour, and recorded their choices during a second round of nest building, where both the asocial (preferred) and social (demonstrated) materials were available. If zebra finches use a *copy-if-dissatisfied* strategy, we expected that males given flexible string and/or those whose

clutches were removed, would shift their material preference toward the demonstrated social material. We further predicted that dissatisfaction induced by recent reproductive failure would exert a stronger effect than dissatisfaction following building experience, consistent with previous findings [27].

These behavioural predictions, however, cannot reveal hidden cognitive mechanisms [10]. To address this, we fit hierarchical Bayesian experience-weighted attraction (EWA) models—originally developed for human strategic behaviour [31]—to infer four latent learning parameters that could jointly underpin material choices:

- ϕ, how rapidly males refine material preferences (asocial information updating);
- λ, how strongly males exhibit material preferences (asocial information weighting);
- ϵ, how elastically males react to deposited social material (social information updating);
- σ, how much males consider asocial versus social information (social information weighting).

These estimates allowed us to capture each nest-building male's decision-making and run forward simulations for two purposes: first, to ensure the model-generated behaviour resembled real data; and second, to test the robustness of our inferred mechanisms in new contexts. In our study, choosing the social material offered no real benefit. But in other contexts, material choice often conveys advantage, such as within-group social signalling (e.g., coloured nest material in birds [22, 32]) or efficiency (e.g., tool use in primates [33, 34, 35]). These choice behaviours may be culturally maintained via social learning [21, 35], and even reflect cumulative culture [34]. To crudely simulate such contexts, we imposed two hypothetical payoff structures: (1) choosing *social pays*, or (2) choosing *social pays more*. Thus, we probed how differential (dis)satisfaction influenced material choice under contexts beyond our study where *copy-if-dissatisfied* is advantageous or increasingly so.

2 Methods

2.1 Subjects

The subjects were 75 male-female adult (> 90 days old) pairs of zebra finches. The two experiments took place in two laboratories (Experiment 1: Saint Mary's Animal Unit, University of St Andrews, UK; Experiment 2: Department of Psychology, University of Alberta, Canada). The zebra finches in Experiment 1 were bred in-house, whereas the zebra finches in Experiment 2 were sourced from a breeder (Eastern Bird Supplies, Quebec, Canada). In both experiments, the zebra finches either participated as subject male-female pairs (Experiment 1: n = 19 pairs; Experiment 2: n = 34 pairs) or as demonstrator male-female pairs (Experiment 1: n = 16 pairs; Experiment 2: n = 6 pairs). All subject pairs were first-time builders. Conversely, each demonstrator pair were, at the start of the current study, experienced builders and already paired together: because the male of the demonstrator pair had previously provided social artefact nests in an unrelated study [30]. None of the demonstrator pairs were the parents or the siblings of the subject pairs. Likewise, no subject pair consisted of siblings. Further details on housing and husbandry are reported in the *Supplementary material*.

2.2 Experimental protocol

In both Experiment 1 and 2, we varied the quality of subject males' first building/incubation experience (hereafter referred to as the dissatisfaction manipulation). Following the dissatisfaction manipulation, subject pairs in both experiments were individually transferred, in blocks, into one side of a test cage that was separated from the other initially by an opaque and removable barrier. The test consisted of four consecutive phases, detailed below.

2.2.1 Dissatisfaction manipulation

In Experiment 1, we manipulated dissatisfaction during nest building by randomly assigning subject males to one of two treatments: building with 100 pieces of either (1) polished 'stiff' string or (2) unpolished 'flexible' string, forming the *Material-Satisfied* (Mat-Sat) and *Material-Dissatisfied* (Mat-Diss) treatments, respectively. All string was off-white, 3 mm in diameter, and cut into 15 cm lengths (James Leaver Co., London, United Kingdom; see Figure 1a in [28]). We placed the string in a single pile at the centre of the cage floor, aligned with the wall-mounted nestbox. The manipulation was considered complete

once males had deposited all 100 pieces into their nestbox. At this point, we removed both the nest and the nestbox (mean number of days ± SE to build a partial nest: Mat-Sat: 5.00 ± 1.98; Mat-Diss: 4.78 ± 1.36). This level of nest-building experience is sufficient to shape subsequent material preferences in this species [27].

In Experiment 2, we manipulate dissatisfaction during the incubation stage of reproduction, after all subject males had completed nest building. Nests were considered complete once females began laying eggs. Males constructed their nests using coconut fibre, which we provided in two 20-gram piles placed on the cage floor, one on each side of the centrally located wall-hanging nestbox. Fibre was replenished as needed during daily nest checks. Upon nest completion, males were pseudorandomly assigned to one of two incubation treatments: either (1) *Incubation-Satisfied* (Inc-Sat), in which they were allowed to incubate eggs, hatch chicks, and rear them to nutritional independence (approximately 35 days of age; [36]), after which we removed the nest and separated offspring when they could be visually sexed (roughly 40-45 days of age; [36]); or (2) *Incubation-Dissatisfied* (Inc-Diss), in which all eggs laid were removed during daily nest checks, preventing incubation. Pseudorandom assignment was structured in dyads: the first male to complete a nest was assigned to the Inc-Sat treatment, the second to Inc-Diss treatment, and so on. Within each dyad, the duration of the manipulation (from first material provision to nest removal and offspring separation) was matched across treatments. We calculated the weight of all nests that we removed, and this proxy for nest-building investment did not differ between treatments (mean nest weight in grams ± SE: Inc-Sat: 39.71 ± 12.49; Inc-Diss: 39.61 ± 13.89).

2.2.2 Test: copy-if-dissatisfied?

Phase 1: preference test. One hour post-light onset on the second test day we provided each subject pair with one pink and one orange bundle of string (n = 25 pieces of string per bundle; James Leaver Co., London, United Kingdom). To prevent nest building, we tied one bundle to the left and one to the right panel of the cage; this location assignment was randomised across subject pairs. Four hours later, we removed both bundles. We then immediately quantified from video recordings how much time each subject male had interacted with—touched with their bill or feet—material of both colours. If he spent $\geq$ 60 seconds interacting with one or both material colours, we considered the coloured material most interacted with to be his preferred material. If his material-interaction time did not reach 60 seconds over the four hours, we repeated this initial preference test the next day, and so on, until the summed material-interaction time across tests reached our preference criterion (mean number of days ± SE to complete Phase 1: Mat-Sat: 1.30 ± 0.21; Mat-Diss: 1.00 ± 0.00; Inc-Sat: 2.57 ± 0.43; Inc-Diss: 2.53 ± 0.52).

Phase 2: pre-observation. Upon completion of Phase 1, we transferred a demonstrator pair into the unoccupied part of the test cage, and allowed the male of this pair to begin nest building in advance of being observed, since the opaque barrier had yet to be removed. We sham-tied 100 pieces of the subject male's non-preferred coloured material midway along one cage-wall side, while on the opposite cage-wall side, we tied 50 pieces of his preferred coloured material (the assignment of material colour to side of the cage was randomised across pairs). The demonstrator male could thus interact with material of both colours but build a nest only with material of the subject male's non-preferred colour. This phase lasted until the demonstrator male had deposited all 100 pieces of the non-preferred material-type into his nestbox (mean number of days ± SE to complete Phase 2: Mat-Sat: 2.10 ± 0.57; Mat-Diss: 1.56 ± 0.18; Inc-Sat: 2.29 ± 0.16; Inc-Diss: 2.40 ± 0.21).

Phase 3: observation. Upon completion of Phase 2, a demonstrator pair received 50 pieces of the subject male's non-preferred material-type sham-tied to the cage wall. The 50 pieces of the preferred subject male's material-type remained tied to the opposite cage wall. The 100 pieces of the subject male's non-preferred material-type previously deposited in the nestbox remained in the nestbox. We then removed the opaque barrier between the cages, allowing the subject male visual access to the demonstrator male, until the demonstrator male had put all additional 50 pieces of the subject male's non-preferred material-type into the nest (mean number of days ± SE to complete Phase 3: Mat-Sat: 1.28± 0.19; Mat-Diss: 1.06 ± 0.25; Inc-Sat: 1.25 ± 0.13; Inc-Diss: 1.20 ± 0.19.).

Phase 4: second-time nest building. Upon completion of Phase 3, we replaced the opaque barrier and we returned the demonstrator pair to their respective colony housing. We placed one pink and one orange string-bundle (n = 25 pieces of string per bundle) in the subject male's cage, mirroring the placement used in Phase 1. Phase 4 ended once the subject male deposited all of one coloured material in his nestbox. His material choice decisions 1 - 25 were subsequently assayed from video recordings. The demonstrated and non-demonstrated coloured material were considered the social and asocial material, respectively.

2.3 Video scoring

All video recordings were scored blind to experimental treatment using Boris version 7.1.3 [37].

2.4 Statistical analyses

We analysed our data using 'rstan' [38] and 'rethinking' [39] in R [40]. Due to subject male drop-outs (see column BC in our original data file at our GitHub repository), our final data set includes 47 subject males (n's of: Mat-Sat: 10; Mat-Diss: 8; Inc-Sat: 14; Inc-Diss: 15). We note that the summary statistics reported above were generated from our final data set.

2.4.1 Behaviour models

To examine how differential (dis)satisfaction influenced males' material choices, we compared (Model 1) first choices and (Model 2) all choices across treatments using hierarchical logistic regression. Both models included individual-level random effects, but Model 2 also accounted for behavioural change over time via trial number and treatment-specific slopes, allowing behaviour to vary across second-time nest building and between treatments.

2.4.2 Cognition models

We built two EWA models: a baseline model without time-varying effects, and a monotonic model that includes time-varying effects. Fig. S1 shows parameter recovery tests used to validate each model.

EWA baseline model. This model consists of three components. The first component estimates males' baseline nest-material attractions $A_{i,j,t=0}$—that is, how preferable nest-material option i (pink or orange string) is to individual j during the initial material preference test ($t = 0$):

$$T_{i,j} = \alpha_j + \beta_j + \omega_j A_{i,j,t=0}. \tag{1}$$

Here, T is the Poisson-distributed total number of touches to option i by individual j; α_j is an intercept term; β_j is a material exposure parameter, reflecting the individual-specific duration of Phase 1; and ω_j is a scaling parameter that weights individual j's baseline attraction scores. Where touch data were missing (n = 19 males in Experiment 1), we did not exclude these individuals, as all parameters were estimated via partial pooling—borrowing information from the group (see Fig. S2).

The second component updates nest-material attractions during second-time nest building:

$$A_{i,j,t+1} = (1 - \phi_k) A_{i,j,t} + \phi_k \pi_{i,j,t}. \tag{2}$$

In words, attraction A to material i for individual j at time $t + 1$ is based on prior attraction $A_{i,j,t}$ and the reward $\pi_{i,j,t}$ from choosing that material at time t, weighted by $\phi_{0\to1}$. Larger values of ϕ indicate faster updating. Thus, ϕ represents *asocial information updating* of material preferences. We initialized $A_{i,j,t=0}$ from the baseline estimates derived in Equation (1) such that $A_{\text{social}} < A_{\text{asocial}}$. Following evidence that nest building activates reward circuits in zebra finches [41], we assigned a reward $\pi = 1$ for choices and $\pi = 0$ for non-choices.

The third component defines the probability of choosing material i by individual j at time $t + 1$ as a convex combination of asocial and social information:

$$P_{i,j,t+1} = (1 - \sigma_k) P_{AS,i,j,t+1} + \sigma_k P_{S,i,j,t+1}. \tag{3}$$

Here, $\sigma_{0\to1}$ controls the weighting of asocial versus social information. Larger values indicate greater consideration—but not necessarily adoption—of social information. Thus, σ represents *social information weighting*.

The probability of asocial influence is defined using a softmax function:

$$P_{AS,i,j,t+1} = \frac{\exp(\lambda_k A_{i,j,t})}{\sum_{m=1}^{2} \exp(\lambda_k A_{m,j,t})}. \tag{4}$$

This transforms attraction scores into choice probabilities. The parameter $\lambda_{0\to\infty}$ controls sensitivity to relative differences in attraction scores: higher values yield more deterministic choices, while $\lambda = 0$ corresponds to random choice. Thus, λ represents *asocial information weighting* of material preferences.

The probability of social influence is based on a modified version of the frequency-dependent conformity function:

$$P_{S,i,j,t+1} = \frac{n_{i,j,t}^{\rho_k}}{n_{as,j,t}^{\rho_k} + n_{s,j,t}^{1}} + \frac{n_{i,j,t}^{1}}{n_{as,j,t}^{\rho_k} + n_{s,j,t}^{1}}. \tag{5}$$

This formulation estimates the influence of deposited social material following demonstration via stimulus enhancement [42], adapted from [8]. Specifically, n_{as} and n_s refer to the cumulative number of asocial and social material pieces deposited by individual j in their nestbox. The parameter $\epsilon_{0\rightarrow1}$ quantifies how reactive individuals are to changes in social-material abundance—conceptually akin to elasticity in economics:

- $\epsilon > 1$: positively reactive (demand for social material increases disproportionately with its observed use)
- $\epsilon < 1$: negatively reactive (demand for social material decreases disproportionately with its observed use)
- $\epsilon = 1$: unreactive (demand for social material is unaffected by changes in nestbox social-material abundance)

Thus, ϵ represents *social information updating*.

EWA monotonic model. The model structure remains as described above, with the key difference that each latent (a)social learning parameter—ϕ, λ, ϵ, and σ—varies over time. Following [14], we imposed a monotonic effects structure on each parameter θ, allowing the model to estimate per-trial step sizes—that is, the direction and magnitude of change across trials. This structure is given by:

$$\theta_{k,t} = \theta_{k,first} + (\theta_{k,last} - \theta_{k,first})\delta_t. \tag{6}$$

Here, θ_{first} and θ_{last} are treatment-level k endpoints, and δ is the cumulative sum of a 24-length simplex, representing the proportion of total change allocated up to trial t. This formulation ensures a monotonic—increasing or decreasing—trajectory over time, allowing the model to capture consistent learning trends as males progressed through second-time nest building.

Note, in both EWA models λ and ϵ were capped at 15 and 10, respectively, because larger values yield near-identical behavioural results and can introduce numerical instability.

2.4.3 Forward simulations

Here, we used agent-based forward simulations, drawing from the posterior distribution of our EWA models, to ask two questions.

Question 1: can we approximate our data? It is possible that, in specifying the EWA models, we mischaracterised structural features of the decision-making process in ways that limit their ability to reproduce observed behaviour. Such mischaracterisations may not be evident from the estimated parameters alone. Instead, these parameters must be embedded in forward simulations to reveal potential mismatches between model assumptions and empirical patterns. To assess this, we matched the number of simulated agents to the sample size in each treatment and assigned each agent treatment-specific values for ϕ, λ, ϵ, and σ, sampled from the model's random-effects multivariate normal distribution. This preserved the empirical correlation structure among parameters. We repeated this process 100 times to account for stochastic variability in simulated behaviour.

Question 2: what would 'choosers' do in novel contexts? Our EWA model estimates characterise a statistical, co-varying population of 'choosers'. We used these estimates to explore how differential (dis)satisfaction might affect their use of asocial and social information in alternative choice contexts. Following the same simulation procedure as above, we simulated 10,000 'choosers' (2,500 per treatment) and examined their behaviour in two hypothetical payoff structures: *social pays*, the social material pays a value of one, while the asocial material pays nothing; *social pays more*, the social material pays a value of two, and the asocial material pays a value of one. See the *Introduction* for the theoretical rationale behind this parameterisation.

3 Results

For all results from our behavioural and computational modelling, we report the posterior mean and 89% highest posterior density intervals (HPDI), which represent the most probable parameter values given the model and data [10]. In the logistic regression models, estimates represent treatment-level effects that incorporate individual-level variation via hierarchical structure, but do not yield interpretable individual-level parameters. By contrast, the EWA models explicitly estimate latent, individual-specific learning parameters (see Fig. S3), which we summarise by treatment group.

3.1 Behaviour

Together, our behavioural results support a *copy-if-dissatisfied* strategy shaped by the relevance of social information to recent experience, with diminished evidence of employment across material choices (Fig. 1).

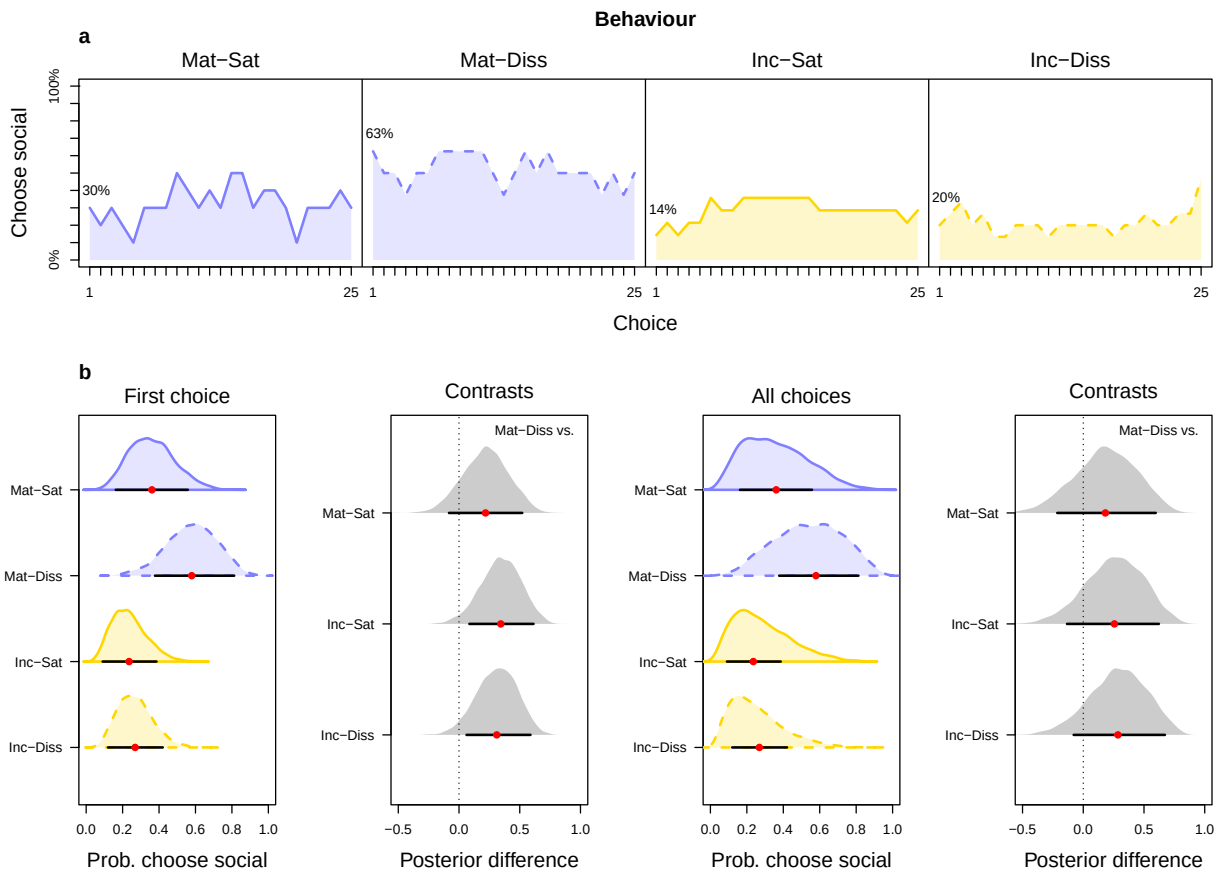

Figure 1. Nest building behavioural results. (a) Mean percentage of males choosing social material over 25 choices for each treatment, shown as lines with corresponding shaded areas. **(b)** Density plots showing posterior estimates of: (left to right) the probability of choosing social material at first choice; contrasts between the Mat-Diss treatment and each of the other treatments at first choice; the overall probability of choosing social material across all choices; and contrasts for these across-choices probabilities relative to Mat-Diss. Red dots show posterior means and black lines denote 89% HPDI.

3.1.1 First choice

The decision to deposit social material first depended on a male's prior experience: 63% of Mat-Diss males chose social material first—at least double the proportion observed in any other treatment (Mat-Sat: 30%; Inc-Sat: 14%; Inc-Diss: 20%; Fig. 1a). Posterior contrasts between Mat-Diss and the other treatments revealed an interactive effect of dissatisfaction and its type on males' first material choice (Fig. 1b). Specifically, males in the Mat-Diss treatment—those given low-quality flexible string—were more

likely to initially choose the social material compared to males in either (un)successful incubation treatment, as indicated by contrast intervals that excluded zero (Mat-Diss versus Inc-Sat: mean = 0.34, 89% HPDI: 0.09–0.62; Mat-Diss versus Inc-Diss: mean = 0.31, 89% HPDI: 0.04–0.57). A similar but weaker effect was observed in the comparison between males given flexible versus stiff string, where the contrast interval narrowly included zero (Mat-Diss versus Mat-Sat: mean = 0.21, 89% HPDI: −0.08–0.52). Biologically, this pattern implies that it was specifically dissatisfaction with material that shifted initial choice toward the social material.

3.1.2 All choices

Though less pronounced than at first choice, the influence of prior experience quality (satisfaction versus dissatisfaction) continued to interact with context (material versus incubation) to shape males' material choices across the full nest-building sequence. Males in the Mat-Diss treatment continued to choose social material more frequently than males in the other treatments, although the magnitude of these differences was smaller (mean proportion of social deposits ± SE: Mat-Sat: 32% ± 10.62; Mat-Diss: 52% ± 13.52; Inc-Sat: 29% ± 11.23; Inc-Diss: 22% ± 8.76; Fig. 1a). Posterior contrasts between males in the Mat-Diss treatment and the other treatments supported this reduced effect (Fig. 2b): although between-treatment behavioural patterns persisted, they were strongest for the comparison with Inc-Diss (mean = 0.30, 89% HPDI: 0.07–0.67), weaker for Inc-Sat (mean = 0.26, 89% HPDI: −0.12–0.65), and weakest for Mat-Sat (mean = 0.18, 89% HPDI: −0.21–0.58).

3.2 Cognition

Together, our cognitive modelling results reveal the dynamic nature of avian nest building: males' material choices were shaped by plastic learning mechanisms that balanced asocial and social cues in response to recent outcomes. All parameter estimates are reported in Table 1; we summarise the key results below.

Table 1. Posterior means and 89% lower (Lo) and higher (Hi) posterior density intervals for each latent learning parameter, by treatment and model. $\bar{\theta}_{\text{baseline}}$, $\bar{\theta}_{t=1}$, and $\bar{\theta}_{t=25}$ denote the average of individual-specific parameter estimates from the EWA baseline model, and from material choice 1 and 25 in the EWA monotonic model, respectively.

Treatment	Parameter	$\bar{\theta}_{\text{baseline}}$	Lo	Hi	$\bar{\theta}_{t=1}$	Lo	Hi	$\bar{\theta}_{t=25}$	Lo	Hi
Mat-Sat	ϕ	0.49	0.29	0.68	0.60	0.56	0.66	0.53	0.49	0.56
Mat-Diss	ϕ	0.53	0.32	0.74	0.60	0.56	0.64	0.57	0.50	0.63
Inc-Sat	ϕ	0.63	0.43	0.82	0.72	0.70	0.76	0.57	0.53	0.58
Inc-Diss	ϕ	0.55	0.36	0.74	0.54	0.49	0.58	0.60	0.54	0.69
Mat-Sat	λ	2.48	1.94	3.00	7.54	0.36	15.00	0.37	0.23	0.70
Mat-Diss	λ	2.62	1.96	3.35	2.35	0.18	15.00	3.36	0.85	5.90
Inc-Sat	λ	4.40	3.44	5.45	6.62	0.36	10.90	6.24	5.45	9.81
Inc-Diss	λ	3.59	2.94	4.27	8.21	0.44	15.00	2.83	0.84	5.15
Mat-Sat	ϵ	1.26	0.08	2.72	1.15	0.64	2.37	0.65	0.09	2.80
Mat-Diss	ϵ	1.50	0.06	3.48	0.97	0.38	1.74	0.83	0.12	2.90
Inc-Sat	ϵ	2.84	0.11	5.77	1.55	1.36	2.46	1.83	0.19	4.50
Inc-Diss	ϵ	1.53	0.09	3.06	0.64	0.30	0.80	1.06	0.15	1.57
Mat-Sat	σ	0.36	0.15	0.56	0.45	0.33	0.49	0.40	0.34	0.47
Mat-Diss	σ	0.23	0.06	0.38	0.34	0.28	0.45	0.39	0.32	0.45
Inc-Sat	σ	0.31	0.09	0.52	0.46	0.40	0.52	0.33	0.31	0.37
Inc-Diss	σ	0.31	0.11	0.48	0.36	0.28	0.40	0.26	0.19	0.30

3.2.1 Asocial information updating (ϕ): how rapidly did males update material preferences?

The EWA baseline model estimates for ϕ were moderate across treatments (Fig. 2, row one, left panels), indicating reasonably fast material preference updating by males. In the EWA monotonic model (Fig. 2, row one, right panels), ϕ remained fairly stable across choices, with a slight decline among most males, except those in the Inc-Diss treatment, who showed a small increase. These time-structured results suggest little overall change in how rapidly males updated material preferences over time.

3.2.2 Asocial information weighting (λ): how strongly did males exhibit material preferences?

The EWA baseline model estimates for λ were highest in the incubation treatments and moderate in the material treatments, indicating stronger material preference expression following reproductive experience (Fig. 2, row two, left panels). In the EWA monotonic model (Fig. 2, row two, right panels), Mat-Sat males showed a sharp decline in λ over time, suggesting a shift toward more exploratory decisions, as reflected by their increased material-choice stochasticity (Fig. 1a). For Mat-Diss males, λ began at a moderate level and increased moderately over time, indicating increasingly stable, preference-based decisions; in this case, directed toward the social material (Fig. 1a). Both incubation treatments maintained high λ values, consistent with their sustained majority-use of the asocial material (Fig. 1a). However, Inc-Diss males exhibited a gradual decline in λ, paralleling their late-trial small spike in social material choice (Fig. 1a).

3.2.3 Social information updating (ϵ): how elastically reactive were males to deposited social material?

The EWA baseline model estimates for ϵ revealed weak positive (>1) social reactivity across males (Fig. 2, row three, left panels), with Inc-Sat individuals showing the strongest estimates, consistent with their early up-tick in choice for social material that then plateaued (Fig. 1a). These results suggests a broad but subtle tendency for demand for social material to increases disproportionately with its observed use. The EWA monotonic model showed that this stimulus enhancement effect remained relatively stable throughout nest building (Fig. 2, row three, right panels), with ϵ showing only slight upward or downward trends—hovering just above, below, or crossing 1 depending on treatment.

3.2.4 Social information weighting (σ): how much did males consider asocial versus social information?

The EWA baseline model estimates for σ were moderate across treatments (Fig. 2, row four, left panels), suggesting predominant consideration of asocial information when choosing material. In the monotonic model (Fig. 2, row four, right panels), σ remained relatively stable in the material treatments but declined somewhat over time in both incubation treatments. Overall, these time-structured results show a sustained, though modest, consideration of social information despite an absence of strong conformity patterns (Fig. 1a)

3.3 Simulation results

3.3.1 Approximation

Together, our forward simulations—matched to treatment sample sizes—show that the EWA baseline model approximated our nest-building data more effectively than the EWA monotonic model, though the difference was modest (Fig. S4). In general, simulated 'choosers' tended to use more of the social material than their real-world counterparts, except in the Mat-Diss treatment where mapping was fairly close. This overestimation likely reflects two structural constraints. First, the reward structure assumes that each choice is equally reinforcing, potentially exaggerating the attractiveness of the social material. Second, in the monotonic model, this reinforcing effect is combined with the imposed cumulative change in parameters over time. In both cases, these constraints may steepen learning trajectories, causing the simulations to overshoot observed social material use. Accordingly, we rely on the more behaviourally-aligned EWA baseline model when probing generalisation beyond our study, recognising that the true value of material choice is likely more individual-specific and nuanced.

3.3.2 Generalisation

Building on the above simulations, we extended our forward simulations to explore two plausible real-world material-choice contexts that deliberately varied in their reward structure (Fig. 3). Here, rather than assuming equal reinforcement, we explicitly tested how differential rewards for social versus asocial material might shape behaviour. Most notably, simulated 'choosers' were more likely to select the social material in the *social pays* context—where only the social material yielded a reward—than in the *social pays more* context, where the social material paid twice as much as the asocial option. Overall, (dis)satisfaction had little effect on choices by 'choosers'. However, recent nest-building experience—rather than incubation experience—tended to reliably shift choice toward the social material, suggesting

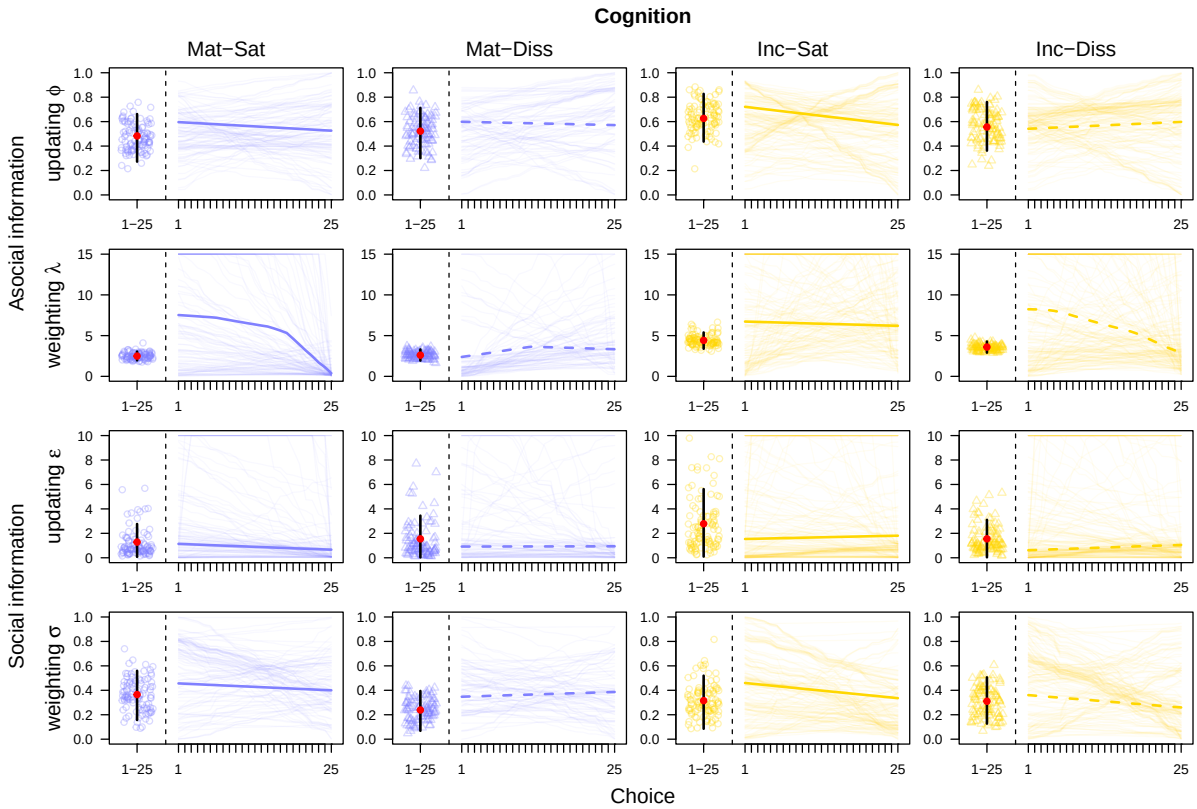

Figure 2. Nest building cognition results. Latent (a)social learning parameters ϕ, λ, ϵ, and σ by treatment and EWA model. Left panels show EWA baseline model estimates, with posterior means (red dots), 89% HPDI (black lines), and 100 posterior draws (open circles or triangles). Right panels show EWA monotonic model estimates, with posterior means (solid or dashed lines) and 10 posterior learning trajectories per male (thin lines). Fig. S3 shows these cognition results at individual-level resolution.

that sensitivity to the relevance of social information may generalise beyond the original experimental context.

4 Discussion

Using a combination of behavioural experiments, Bayesian cognitive modelling, and forward simulations, we set out to examine strategic social learning in nest-building zebra finches—specifically testing the *copy-if-dissatisfied* strategy, and modelling the underlying cognitive mechanisms plus their potential generalisability. Below, we discuss our behavioural results, cognitive model findings, and exploratory simulation outcomes.

4.1 Nest-building zebra finches *copy-if-dissatisfied* with material experience

After observing conspecific nest building, zebra finches chose more of the demonstrated social material—particularly for their first material choice—if they had previously experienced low-quality material during nest building. Notably, neither high-quality material nest-building experience nor reproductive outcomes—whether successful or unsuccessful in incubation—led to as much social material use as that observed in males with poor nest-building material-experience. Together, these behavioural results suggest nest-building zebra finches are more likely to use social information about 'what to choose', especially initially, when their own material-use experience has been dissatisfactory, consistent with a *copy-if-dissatisfied* strategy.

The influence of individual dissatisfaction on social information use has previously been demonstrated experimentally in several taxa, including bats [43], beetles [44], bumblebees [45], and rats [46].

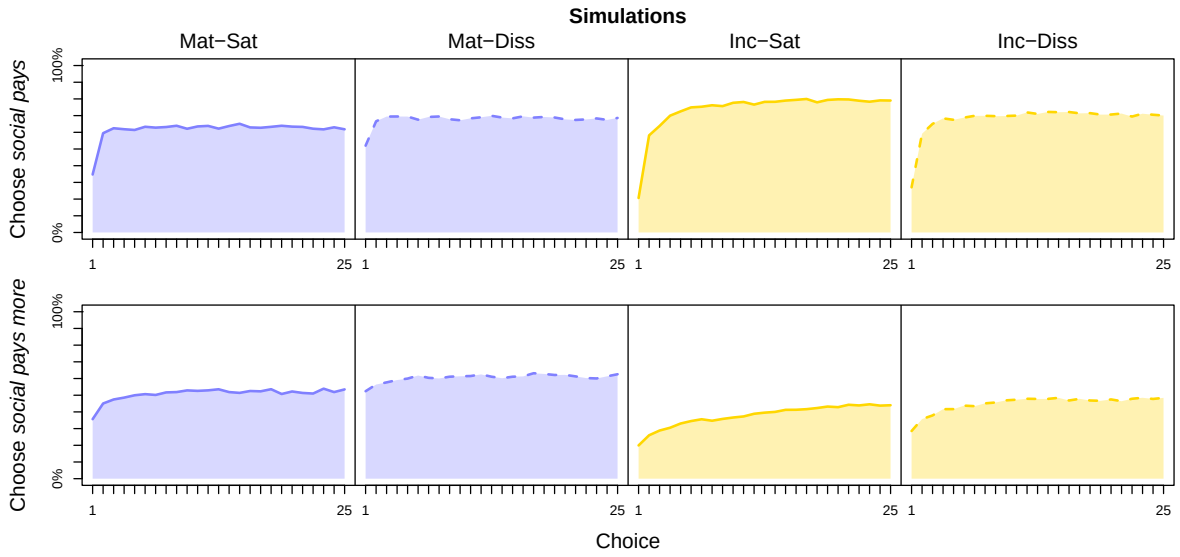

Figure 3. Nest building forward simulation results. Mean percentage of 'choosers' (n = 2,500 per treatment) choosing the social material across 25 choices—shown as lines with corresponding shaded areas—under varying reward contexts. In the upper row, the social material paid a value of one, while the asocial material paid nothing; the *social pays* context. In the lower row, the social material paid a value of two, while the asocial material paid a value of one; the *social pays more* context.

More broadly, the use of strategic social learning rules to filter information and optimise learning opportunities is both theoretically and empirically supported—examples include biasing social learning toward kin or adults [47, 48], or monitoring the frequency or reward-payoffs of others' choices [13, 16]. We extend this general literature by showing not only that dissatisfied animals use social information strategically, but also that this strategising appears adaptive—that is, fine-tuned to expected utility.

Here, *utility* refers to the potential benefit of copying conspecific-presented nest material. Given that zebra finches associate nest-building efficacy with material properties—such as rigidity, which may influence reproductive success [27, 28]—our finding that males with prior experience using 'bad' flexible string tended to choose more of the demonstrated social material is consistent with this predicted association. In contrast and against our prediction, males whose clutches were removed used less social material, suggesting they may have attributed their reproductive failure to other causes, such as nest predation (birds learn this association: [24, 49]). If so, different types of social information—such as cues about where to nest—may have been more relevant to them, a hypothesis open to future experimental testing. The relatively low use of social material by satisfied males likely reflects the absence of an adverse first-time building or incubation experience, consistent with a simple win-stay heuristic. Future research could investigate whether this heuristic breaks down when characteristics of demonstrators, such as relatedness or age [1], are experimentally manipulated.

Nest-building zebra finches, then, did not apply a blanket *copy-if-dissatisfied* strategy, nor did they copy exclusively when they did. We observed individual variation in social material use over time, with the highest observed use being only 63% by Mat-Diss males on their first material choice. This relatively modest initial level of copying may reflect the absence of any functional—and thus reinforcing—difference between the asocial and social material [25]. Importantly, the individual-level and temporal variation we observed underscores the dynamic nature of asocial and social information use—a process our cognitive modelling aimed to capture.

4.2 Nest-building zebra finches dynamically inform their material choice

We developed dynamic EWA learning models [8, 31] to estimate how latent asocial and social learning parameters shaped nest-building zebra finches' material choices, including one version that allowed parameters to change over time. However, the time-structured model was marginally less successful at approximating the real behavioural data (see above), so we focus here on results from the more robust baseline model.

All zebra finches exhibited moderately high *asocial information updating* (ϕ)—they readily revised their material preferences based on recent material choices. This result aligns with the only other study, to our knowledge, that estimated ϕ in birds within a social learning context, which similarly found high responsiveness to individual choice experience, although this declined with age [13]. While our study was not designed to test age effects, the fact that zebra finches learn nest building both asocially and socially [20, 24, 25, 26] suggests it is plausible that resistance to new nest-related information increases with age. This possibility merits further investigation, particularly since recent EWA simulations show ϕ can influence the speed at which socially acquired behaviours are produced [50], implying that younger birds may conform more quickly than older individuals to local architectural traditions [21, 23, 32].

Estimates for *asocial information weighting* (λ) were high across all zebra finches and even higher in the incubation treatments than in the material treatments. This implies that males generally exhibited strong material preferences and switched infrequently between materials. In the computational reinforcement learning literature[51, 52], such choice patterns are typically interpreted as indicators of high reward sensitivity or low exploration—reflecting risk-sensitive or deterministic behaviour [11, 14, 50]. Although our EWA model rewarded males equally for both materials (see *Statistical analyses*), zebra finches received no explicit material-choice rewards during the study. However, nest building has been shown to activate reward circuits in zebra finches [41], suggesting dopaminergic mechanisms may underlie our males' apparently conservative material preferences—in other words, males may have largely stuck with the material they 'liked'.

All zebra finches exhibited modest (>1) *social information updating* (ϵ): with each social material deposit, they became slightly more likely to choose it, indicating a tendency to demand more of this socially-enhanced stimulus rather than ignoring or reducing interest. This stimulus enhancement effect could be estimated due to the adaptability of the EWA modelling framework, which accommodates a wide range of mathematically defined processes—including age- or payoff-based biases [8, 14]—and can be tailored to contexts like ours, where social demonstration occurs outside of group-level conformity dynamics. More broadly, computational modelling encourages researchers to formalise hypotheses about learning processes, supporting more precise and testable accounts of behaviour than those offered by catch-all terms; for example, 'behavioural flexibility' [11, 53].

Finally, when comparing *social information weighting* (σ) to the asocial parameters (ϕ and λ), zebra finches overall placed greater weight on asocial information, though they did consider both types of cues. That the EWA model captured these nuanced influences represents a methodological advance over previous work on zebra finches, where—lacking evidence of strong conformity—social influence was often inferred from initial material touches alone [20, 25, 54]. Our generative forward simulations, discussed below, suggest in contexts where social material confers a clear payoff advantage, consideration of social information could outweigh that of asocial cues more strongly than in the present study.

4.3 Beyond nest-building zebra finches

In simulations exploring how differential (dis)satisfaction influenced choice behaviour in new contexts where rewards varied by material, we found that this prior experience had minimal impact; instead, choices were primarily driven by payoffs.

Perhaps the most striking result emerged in the *social pays* context, where only the social material yielded a reward: here, 'choosers' selected the most social material. This pattern highlights how payoff-sensitive *asocial information updating* (ϕ) can steer behaviour away from costlier options—since choice behaviour feeds back to shape material preferences (see Equations 2 and 4)—and suggests population-level (cultural) differences in material use (e.g., [22, 32, 33, 34]) can emerge even without explicit strategic social learning rules. Supporting this, experimental data show combining asocial payoff sensitivity with conformity bias can produce adaptive foraging traditions in wild birds without the need for strategising based on others' payoffs [13].

Notably, in the *social pays more* context—where the social material offered twice the reward of the asocial one—'choosers' following (un)successful incubation used less social material than in the *social pays* context. This counterintuitive result suggests simply increasing the relative payoff of a social material-option may not be sufficient to drive stronger use of it. In humans, cumulative improvements in material technology are thought to arise from a combination of mechanisms, including copying, innovation, exploration, and biases such as success- or prestige-bias [55, 56]. A similarly multi-faceted process is thus likely required to scaffold supposed cumulative improvements in material-use behaviour in other animals (e.g., [34]). Indeed, wild birds learning a high-rewarding multi-step foraging task rely on social learning of the lower-rewarding components, followed by asocial chaining of those steps through practice [57].

These simulation-derived data should, however, be interpreted with caution, given our limited sample—both in size and taxonomic scope—and the reductionist structure of our computational setup. Future work should improve on these limitations, perhaps beginning with better individual-level approximations of material-choice evaluations.

4.4 Conclusions

Long assumed to be an entirely innate behaviour, avian nest building is now firmly recognised as shaped by individual learning, with growing evidence for social influences and, more recently, the emergence of architectural culture [20, 21, 22, 23, 24, 26]. Our study adds to this picture by showing nest-building zebra finches follow a *copy-if-dissatisfied* strategic social learning rule, but only when the social information aligns with their recent experience—suggesting they recognise the utility of such information. Crucially, we identified the underlying latent learning mechanisms that dynamically drove these decisions—two asocial and two social parameters—thereby laying to rest any lingering doubts about the cognitive basis of birds' nest building. We then validated these mechanisms using generative simulations, demonstrating that our baseline model outperformed a time-varying alternative. This outcome underscores the value of simulation-based model falsification for identifying the cognitive model that best captures real-world decision-making [9]. Finally, by extending the more robust, behaviourally aligned model to simulated 'choosers' in novel reward contexts, we generated preliminary predictions about drivers of material-use behavioural variation, offering a tentative theoretical foundation for future comparative work across taxa and contexts. We hope our open-access analytical approach and accompanying insights, alongside growing recognition of cognitive and phenotypic parallels between nest building and tool use [21, 23, 24, 58, 59, 60], will encourage further research into the learning dynamics of animal material-use behaviour, particularly from a computational framework [15].

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Supplementary material for the manuscript

Dynamic strategic social learning in nest-building zebra finches and its generalisability

Alexis J. Breen, Tristan Eckersley, Andrés Camacho-Alpízar, Connor T. Lambert, Gopika Balasubramanian, Susan D. Healy, Richard McElreath and Lauren M. Guillette

Corresponding authors: Alexis J. Breen (alexis_breen@eva.mpg.de); Lauren M. Guillette (guillett@ualberta.ca)

GitHub repository: https://github.com/alexisbreen/Dynamic-nest-building

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Further details on housing and husbandry

When not participating in the current study, all subject and demonstrator male-female zebra finch pairs were housed in same-sex free-flight colony housing; more specifically, either in colony rooms (Experiment 1: males, 318 × 312 × 230 cm; females, 438 × 251 × 230 cm) or in colony cages (Experiment 2: males and females, 165 × 66 × 184 cm).

During their respective experiment, subject male-female pairs were first housed in training cages during their experiment-specific dissatisfaction manipulation (Experiment 1: 75 × 75 × 40 cm; Experiment 2: 50 × 50 × 100 cm). After this, they were housed in testing cages (Experiment 1 and 2: 50 × 50 × 100 cm). Demonstrator male-female pairs, by contrast, were only housed in testing cages. Training cages were placed together in one, or between two, experimental room(s) (Experiment 1 and 2, respectively). In either case, subject male-female pairs could only hear and not see one another due to opaque between-training-cage barriers. Testing cages were placed in a pair in one, or in three different, experimental room(s) (Experiment 1 and 2, respectively), roughly 10 cm apart and back-to-back, with a removable opaque barrier allowing for control of visual access between sets of testing cages. Depending on the experiment, training and testing cages were either fitted with, respectively, one and three cameras (Experiment 1; Spy Camera CCTV, Bristol, United Kingdom), or, each with three cameras (Experiment 2; mini BNC cameras, OSY CAMS), to habituate or record subject male's behaviour on a corresponding laptop computer. All training and testing cages each contained six perches, two food and two water bowls, and a wooden open-faced nestbox (both experiments: 12.5 × 12 × 12 cm), which was hung midway on the back cage panel.

Irrespective of housing, all subject and demonstrator male-female zebra finch pairs had *ad libitum* access to seed, vitamin-supplemented water, oystershell grit, cuttlefish bone, and vitamin block; plus fresh spinach and/or spray millet three times per week. The zebra finches were kept at approximately 19–24°C, on a 14:10 light:dark hour cycle, with humidity levels between 30–50%. Finally, Experiment 2 subject male-female pairs (plus their offspring) received fresh egg mix, daily.

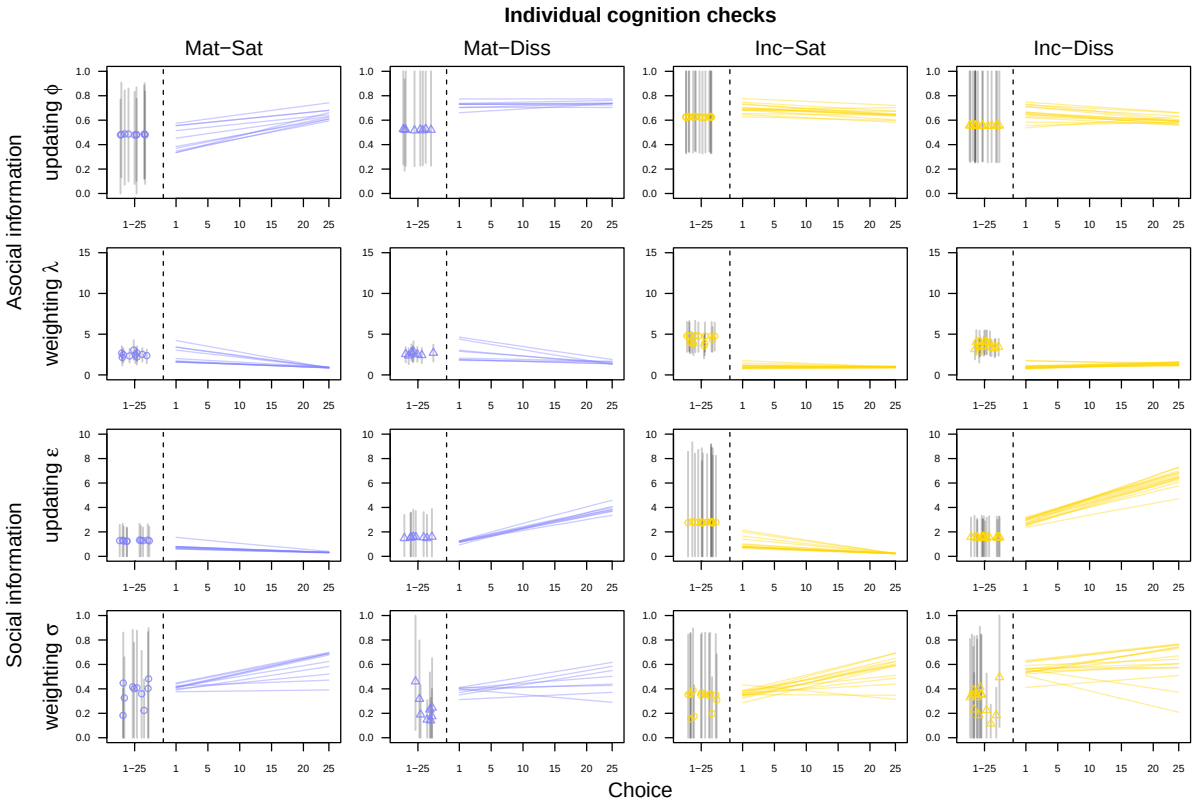

Figure S1. EWA model validation. Prior to fitting our EWA baseline and monotonic models to the empirical data, we validated both models via standard parameter recovery tests using simulated data matched to our treatment sample sizes. This figure shows one such test. For the baseline EWA model, parameters were specified as: $\phi = 0.5$, $\lambda = 3$, $\epsilon = 1$, and $\sigma = 0.5$; with both between and within treatment, and between experiment variation. For the monotonic EWA model, all parameters were identical except for ϵ, the elasticity of demand for social material, which was designed to vary over time. Specifically, to model a differential (dis)satisfaction effect, we simulated distinct behaviours for satisfied and dissatisfied 'choosers': Mat-Sat and Inc-Sat 'choosers' decreased their demand by approximately 80%, while Mat-Diss and Inc-Diss 'choosers' increased their demand by approximately 500%. Both models recovered these specification dynamics within a reasonable range. Left panels display EWA baseline model estimates: open circles or triangles represent posterior means for each 'chooser', with black lines indicating 89% highest posterior density intervals. Right panels display EWA monotonic model estimates: each line represents the posterior mean trajectory across 25 choices for a single 'chooser'.

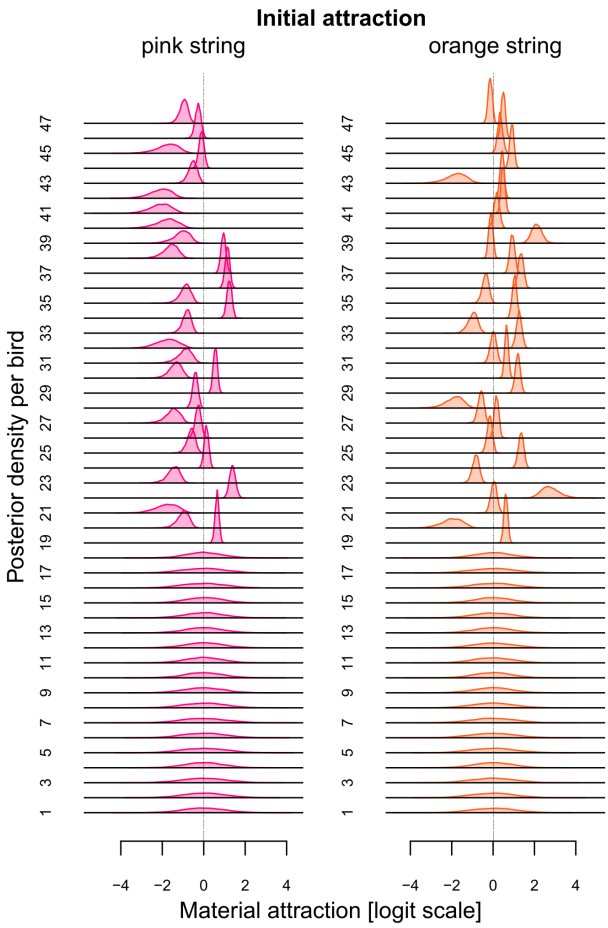

Figure S2. Initial material attractions. Density plots showing posterior distributions of initial pink and orange string attractions for subject males (see Equation 1 in the main text). Note that the wider distributions for Birds 1–18 reflect the absence of touch data from Experiment 1. Estimation for these individuals remains possible through partial pooling, which borrows strength from the group-level structure.

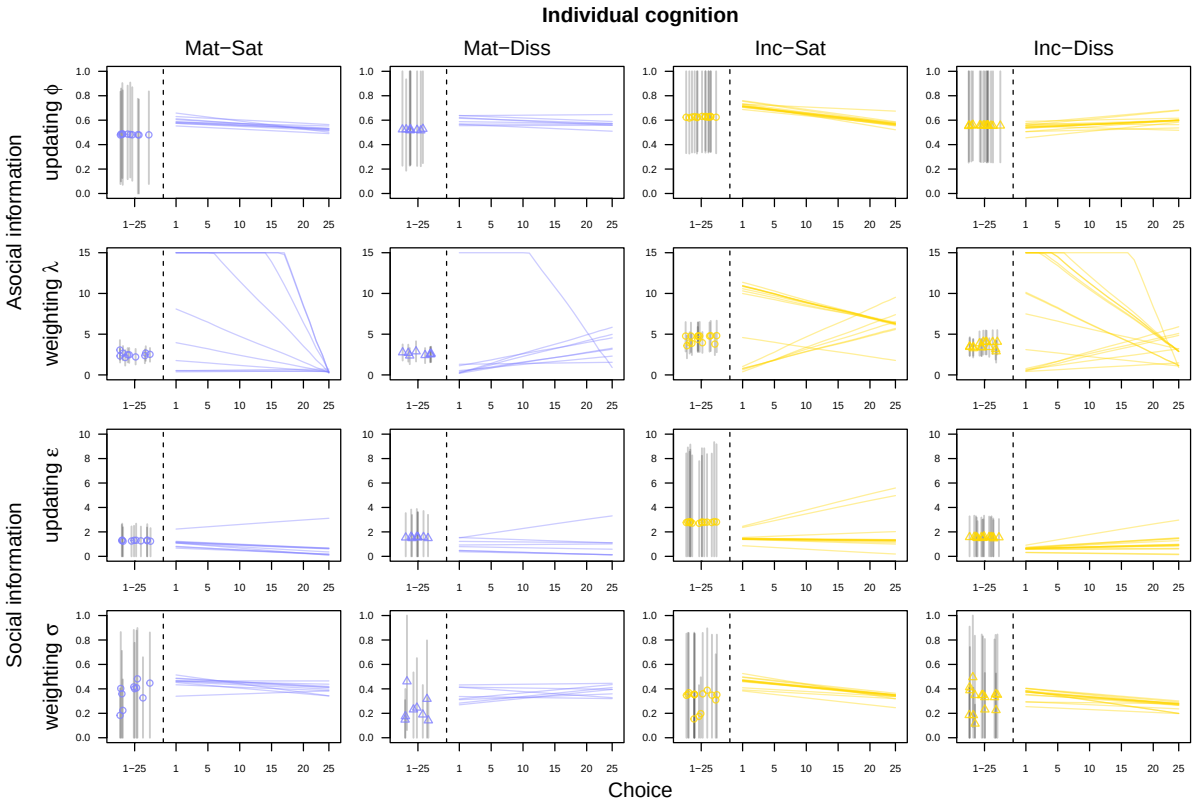

Figure S3. Individual-level cognition results. Latent individual-level (a)social learning parameters ϕ, λ, ϵ, and σ by male, treatment, and EWA model. Left panels display EWA baseline model estimates: open circles or triangles represent posterior means for each male, with black lines indicating 89% highest posterior density intervals. Right panels display EWA monotonic model estimates: each line shows one male's posterior mean trajectory across 25 choices.

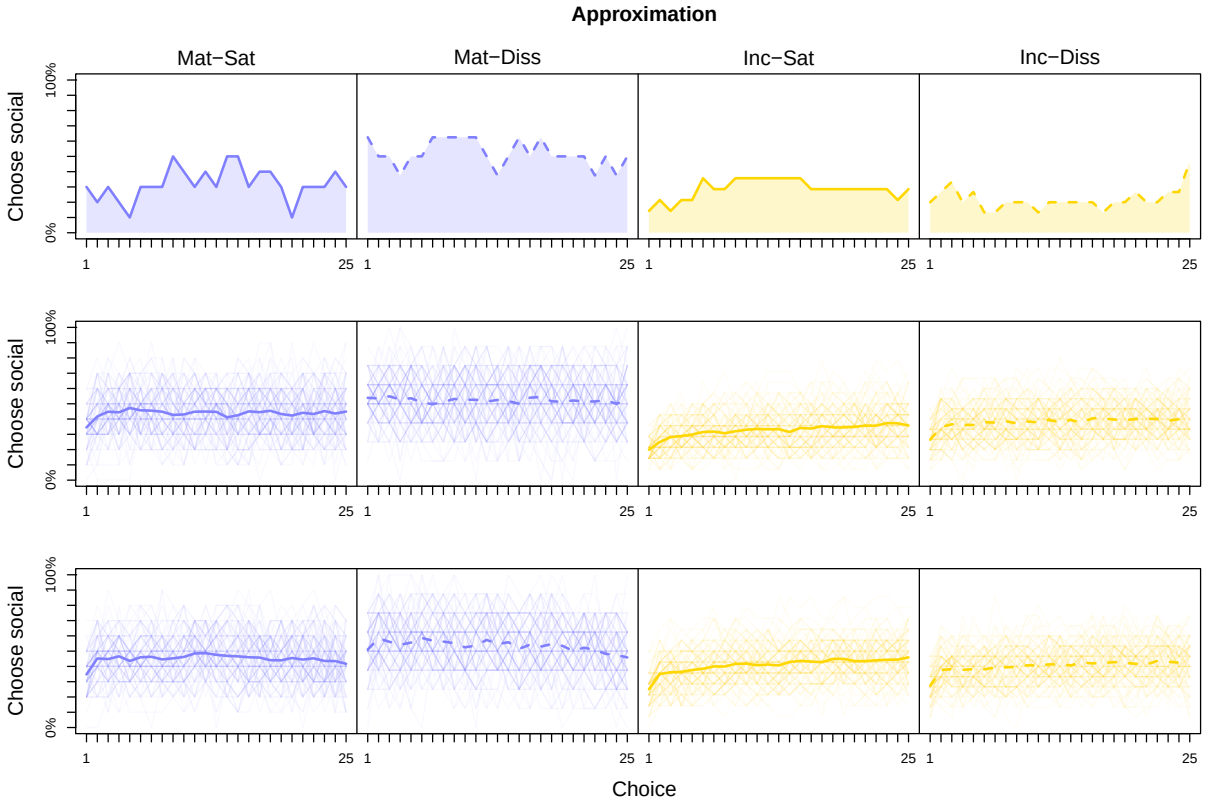

Figure S4. Forward simulation approximation results. Mean percentage social-material choice across 25 choices by treatment for: (top row) real birds; (middle row) 'choosers' generated from the posterior of the EWA baseline model; and (bottom row) 'choosers' generated from the posterior of the EWA monotonic model. Thick solid and dashed lines indicate the overall mean percentage of social material use across choices. Thin lines in the middle and bottom rows show the mean percentage social material use across choices for each simulation (n = 100). Simulations were matched to the sample size of each treatment. Both models tend to overestimate social material choice compared to the behaviour of real birds, except in the Mat-Diss treatment. However, 'choosers' generated from the EWA baseline model posterior slightly overshoot social material use to a lesser degree in the incubation treatments. See the main text for further discussion.