Exploring the factors underlying adaptive social plasticity in foragers using an agent-based model

***Running title**: *Modeling adaptive social plasticity

Sanjay Prasher[1*] (prashesy@mail.uc.edu, 513-885-0800) & Elizabeth A. Hobson[1]

[1] Department of Biological Sciences, University of Cincinnati, Cincinnati, OH

Word count: 6203

Abstract

Recent studies in group-living species suggest that being a valuable group member (a source of information or other resources) should increase social connectedness. This is because individuals may recognize and associate more with valuable individuals to increase the chances of benefiting from their activity, a process we refer to here as adaptive social plasticity. However, it is still unclear what minimum cognitive abilities are required for animals to alter their social interactions based on the value provided by different group members. We varied the cognitive skills of individuals in an agent-based model and evaluated changes in how access to a food resource impacts an informed agent's social connectedness. We modeled a social foraging scenario in an arena with one food patch, which only one informed individual (i.e., producer) can make accessible. Agents' movement decisions were driven by three cognitive-based parameters: *attention* (probability of perceiving successful foragers), *preference* (probability of following successful foragers), and *memory* (number of time steps a successful forager was remembered). To understand what combination of these parameters may facilitate adaptive social plasticity, we compared the producer's strength (number of interactions) in a proximity network and the foraging success of non-producers between simulations with different combinations of parameter values. We found that non-zero values of each of our parameters are necessary for increases in producer strength and non-producer foraging success to occur. The largest increases in producer strength were seen at intermediate memory values and high values of attention and preference. Unless foragers were programmed to be able to move directly to the food patch when it was accessible to them, a non-zero value of memory was needed for them to experience an increase in foraging success. Furthermore, relationships between attention, memory, and foraging success were influenced by preference values, with the highest foraging success achieved at low to intermediate values of preference. Our results highlight the necessity of certain cognitive skills for animals to take advantage of the foraging success of their group mates, and scenarios in which rigid following behavior may lead to less beneficial results for foragers. This model lays the groundwork for further investigations into the cognitive and environmental factors expected to influence a feedback process between social connections and the value provided and received by group members.

Introduction

Social connectivity is a result of the actions of individuals, and recent work has drawn attention to the existence of feedbacks between individual social decisions and their social environment (Hobson and DeDeo 2015; Hobson et al. 2019; Kulahci and Quinn 2019; Cantor et al. 2021). For instance, individuals may respond to benefits provided by group members by choosing to affiliate more with group members that are able to solve novel foraging tasks (Fruteau et al. 2009; Kulahci et al. 2018), which is likely to then influence the transmission of the skill through the group. We will refer to this process of altering social interaction patterns in ways that increase the benefits of interactions or decrease the costs as *adaptive social plasticity* (see also Kings et al. 2023). This process may occur as group members differentially access valuable information or social characteristics that change the benefits of interacting with others.

Social decisions that aim to optimize the costs and benefits that individuals experience in their social environment may be influenced by cognitive abilities in some species (Wascher et al. 2018; Hobson et al. 2021), with variation possible both at the individual level as well as varying across different species. However, cognitive abilities are difficult to manipulate in empirical experiments without the use of invasive procedures. As an alternative, we can infer what individuals may know about their group members, and the underlying cognitive mechanisms involved, based on how they interact. For example, social interaction patterns can provide insight into what information animals may use when making decisions such as with whom to associate. In one experiment, Kulahci et al. (2018) inferred that lemurs (*Lemur catta*) may have directed more affiliative interactions toward group members that were able to open a novel task because they perceived those group members to be knowledgeable individuals. In another study of social plasticity, Kings et al. (2023) found jackdaws (*Corvus monedula*) associated more with individuals that facilitated a greater reward in a social foraging manipulation. The authors argue their results are explained by individual discrimination and associative learning and find no evidence that jackdaws understood the causal role of their social partners in gaining rewards (Kings et al. 2023). While these approaches can provide indications of potential cognition underlying adaptive social plasticity, they cannot detect it or its effects on social decision-making directly.

Agent-based simulations can help in inferring connections between sociality and cognition because they allow us to build a virtual world containing agents that follow defined rules for engaging with their physical and social environment. Using such simulations, we can determine what social patterns are likely to emerge from the effects of specific cognitive skills that are programmed into agents. To understand the influence of cognitive skills on adaptive social plasticity, we can model a scenario in which one agent provides a valuable service to its group members. We can then observe what combination of cognitive skills results in changes to the social interactions received by the valuable social partner and whether agents simultaneously experience greater benefits. Modeling approaches have been used in combination with empirical studies to understand foraging dynamics. Social foraging is commonly understood as a producer-scrounger dynamic, where individual group members may take the role of producer, those that find or access food independently, or scrounger, those that take advantage of food patches found by others (Barnard and Sibly 1981). Models of producer-scrounger dynamics have incorporated cognition in the form of learning rules that allow foragers to adjust their strategy use according to its payoffs (Beauchamp 2000; Dubois et al. 2010; Katsnelson et al. 2012; Afshar and Giraldeau 2014). Researchers have shown that these changes can also happen during empirical experiments, where animals can learn to adjust their use of the scrounging tactic to improve their foraging efficiency (Morand-Ferron and Giraldeau 2010; Afshar et al. 2015; Reichert et al. 2021).

We built an agent-based model to evaluate how cognitive skills interact to facilitate adaptive social plasticity in a foraging context. Our model was designed to resemble empirical experiments that have investigated how changes to the value of group members lead to changes in social interactions received by those group members (Kulahci et al. 2018; Blersch et al. 2024). In such experiments, the value of a group member is manipulated by giving it special access to a food source (a novel foraging task or automated feeder). We tested whether changing the value an individual provides to its group could cause its group members to adaptively respond and change how they interacted with the newly-valuable individual. In our model, we manipulated an individual's value by changing which individuals could access a food patch. After creating a group of foragers with a single producer and one food patch, the model proceeded in three phases. In Phase 1, the food patch was accessible to any agent that found it. In Phase 2, only the producer had the ability to access the food (analogous to an experimental manipulation). Once the food in this phase was accessed by the producer, all other individuals could temporarily access the food patch as well, making the foraging success of scroungers in Phase 2 dependent on the producer's actions. In Phase 3, we again allowed all individuals access to the food patches. Throughout all three phases, agents could perceive and remember others who ate at the food patch and used this information to make movement decisions (reflecting a scenario in which individuals follow group members that they associate with food or believe to be successful foragers).

We investigated three main questions with this model. First, how did cognitive parameters influence changes in the producer's connectedness in a social network based on proximity relationships when its social value was increased? Second, what parameter combinations allowed changes in the producer's connectedness to persist after its social value was removed? Third, how did parameters influence the foraging success of scroungers? With the first two questions we aimed to understand the conditions leading to social plasticity, specifically what combination of cognitive skills led to adjustments in social interactions and persistence of these changes. With the third question we aimed to understand the conditions that allowed scroungers to make the most adaptive decisions, adjusting their social interactions with the producer in a way that benefitted them.

Methods

We used the software Netlogo version 6.4.0 (Wilensky 1999) to build a model of the social dynamics of a group of agents who use simple rules for following successful foragers. The purpose of this model is to evaluate the essential cognitive skills required for animals to adaptively change their associations with group members based on their perceived social value. We provide an overview of the model below. A more detailed description, following the ODD (Overview, Design concepts, Details) protocol (Grimm et al. 2006) as updated by (Grimm et al. 2020), can be found in Supplemental Information 1.

Model entities

Agents in the model represent individually identifiable animals composing a social group. In each simulation, one agent is assigned the role of producer while the remaining agents play the role of scrounger. The producer and scroungers all have variables that track their energy levels ("energy"), store the identity of the successful forager that they perceived ("sf-seen"), and track the number of time steps since the successful forager was first perceived ("sf-seen-timer"). Finally, there is a single food patch in the center of the arena which holds resources that can be temporarily depleted by foragers.

Model parameters

We modeled three key parameters, which we call *attention*, *preference*, and *memory*, that we hypothesize are necessary for adaptive social plasticity to occur. To respond to the activity of group members, individuals must first perceive this activity and decide to adjust their associations with those social partners. If changes in social connections are to persist, individuals must be able to recognize and remember the group members of high social value. *Attention* in our model represents the likelihood of perceiving the foraging activity of others, *preference* represents the propensity to follow successful foragers, and *memory* reflects how long agents remember the successful forager they perceived. Higher attention and preference values in our model may be thought of as representing a greater reliance or value placed on social information. The ability to perceive the foraging activity of others is independent of the distance between agents as we are modeling an experimental scenario in which a group forages in a closed arena where there are no impediments to an individual's ability to observe its group members. In the case of preference, higher values may also be thought of as representing a closer adherence to a “follow if successful” movement rule (like the “copy if successful” social learning strategy Laland 2004). For simplicity, our preference parameter does not explicitly incorporate a learning mechanism by which agents prefer to follow successful foragers. Finally, memory, the storage and retention of information over time, is a fundamental domain-general cognitive ability that underlies a variety of social behaviors. In our model, higher values of memory allow the effects of attention and preference to persist for more time within a simulation.

We also incorporated and analyzed the effects of group size and direct attraction to food in our model and how the effects of the above cognitive skills may interact with these. Group size controls the number of agents in the simulation to represent a range of possible small group sizes. We expected larger changes in the producer’s strength between Phase 1 and Phase 2 of the model with increasing group size, but a negative relationship between the foraging success of agents and group size due to competition for resources. All simulations had one producer but differed in the number of scroungers. *Asocial-information* is a binary parameter (it could be enabled or disabled within a simulation) that controls whether scroungers are able to move directly toward the food patch when their energy level falls below a specified value. Having asocial-information enabled may be thought of as representing a scenario where scroungers have independent knowledge about food location and availability. This parameter allowed us to compare model outputs for situations where agents are able to easily find food even without responding to the foraging success of others (asocial-information enabled) and where agents have no independent knowledge of food availability (asocial-information disabled).

Initialization and dynamics

At initialization, the arena is resized according to the total number of individuals in the group, such that spatial density is kept constant across group sizes. Although this increases the area that larger groups would have to explore to find the food patch, the overall scale of the arena remains small and a larger number of individuals would provide more chances to find the food patch. The total number of agents in a simulation is determined by the *group-size* parameter (Table 1), where one agent is a producer and the rest are foragers; all individuals are assigned a random start location. Each agent receives an initial energy value, which can be thought of as reflecting its hunger level, and the food patch is created with a consistent initial amount of resources.

Agents make movement and foraging decisions on discrete time steps (see Fig. 1 for details). The producer goes first and follows its own set of rules based on its current energy level and location with respect to the food patch. If the producer's energy is high, it will take a step in a random direction, if its energy is low it will move directly toward the food patch, or feed if it is standing on the food patch. Feeding involves an agent increasing its own energy level while simultaneously decreasing the resource level of the food patch by a fixed amount. In addition to energy level and location, scrounger movements are influenced by their ability to remember one agent at a time that they saw feeding and are governed by four parameters: (1) *attention*, (2) *preference*, (3) *memory*, and (4) *asocial-information* (see Table 1 for definitions). Before making a movement or foraging decision, each scrounger first compares the value of its sf-seen-timer to the memory parameter and updates its sf-seen (identity of an observed successful forager) and sf-seen-timer variables. Each scrounger then follows a series of steps to determine whether to feed, move toward the successful forager it remembers, move directly to the food patch (only possible when the asocial-information parameter is enabled), or move in a random direction. Agent movements can result in multiple agents temporarily occupying the same spatial location. All agents' energy levels decrease by one at the end of their turn no matter what action they take.

Once all agents have completed an action in the current time step, a final procedure for updating their sf-seen variable is run if there was at least one agent that fed in the current time step (Fig. 1). For simplicity we allowed each agent to remember just one successful forager at a time for the number of timesteps set by the memory parameter. Only after that time had passed could an agent change which individual was stored as its sf-seen.

The model consists of three major phases, each lasting 100 time steps, for a total length of 300 time steps per simulation, representing foraging interactions over a short timescale. In Phase 1, all agents can access the food patch themselves, which provides an opportunity to measure baseline levels of association. In Phase 2, the food patch must be accessed by the producer before any other agents are able to feed, which provides an opportunity to measure levels of association when the producer has added social value. Finally, in Phase 3, all agents are once again able to access the food themselves, providing a post-manipulation period we can use to assess the persistence of effects from Phase 2. In all three phases, the food patch can be depleted by foragers and will reset to its initial resource value once its resource value falls below a set threshold, which parallels experimental designs with artificial feeders which can be periodically reset. In Phases 1 and 3, once the food patch is depleted below the threshold value, it disappears for five time steps after which it is reset to the initial resource value by any agent stepping on it. In Phase 2, once the food patch is accessed by the producer, it remains accessible to all agents until it is depleted below the set threshold (thus the foragers receive a benefit from the producer’s foraging success). After passing the threshold, the food patch resets to the initial resource value and must be made accessible by the producer again. The threshold to reset the food patch was kept constant across group sizes to reflect increasing competition for food with increasing group size (see Supplementary Figure S1 for information on the number of food patch resets with group size).

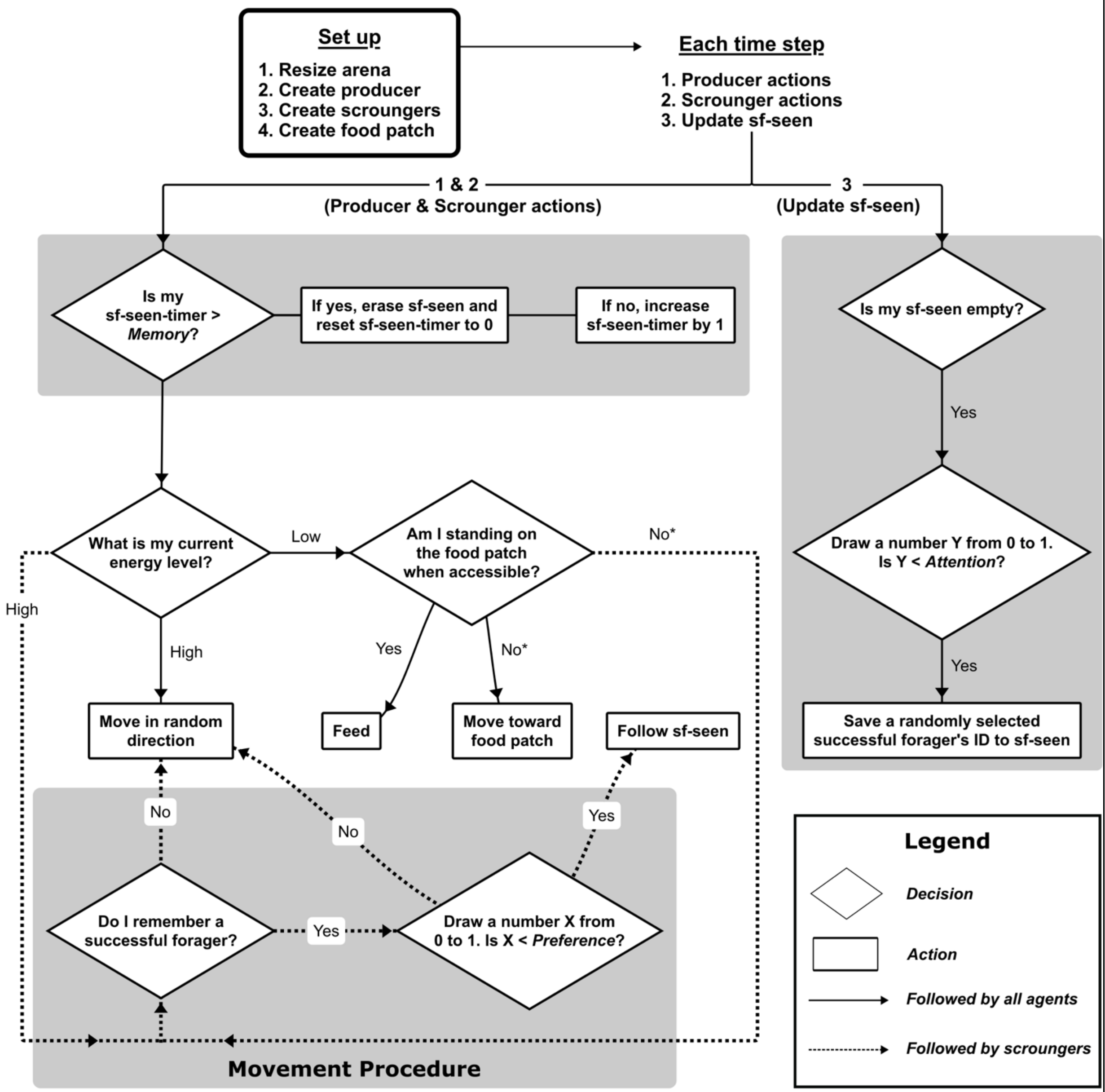

Figure 1. Flowchart depicting the decision-making process of agents at each time step within a model run. Prompts within grey shaded areas are only relevant to the movement decisions of scroungers. The step to update the sf-seen variable is only executed if at least one agent chose to feed in the current time step. The same steps are taken no matter which phase of the model is running. *Scroungers move toward the food patch if it is currently accessible and asocial-information is enabled. If either of these conditions is not met, they follow the movement procedure outlined in grey.

Table 1. Global model parameters

Parameter	Meaning	Values
Group-size	Total number of agents in a simulation	3, 6, 10, 15
Attention	Probability of perceiving successful foragers	0, 0.25, 0.5, 0.75, 1
Preference	Probability of following successful foragers	0, 0.25, 0.5, 0.75, 1
Memory	Number of time steps a successful forager is remembered	0, 50, 100, 150, 200
Asocial-information	Whether scroungers can move directly to food	Enabled, disabled

Outcome measures

For each time step of a simulation, we extracted the list of foragers that were within two spatial units of each agent. Each instance of a forager in proximity to another agent was considered a proximity interaction. We also extracted the identities saved in each agent's sf-seen variable and each agent's energy level.

Using these data, we first determined the social connectedness of the producer in each model phase. We defined social connectedness within each phase as the sum of the producer's number of proximity interactions across each time step in that phase (i.e., strength in the proximity network). We calculated the difference in the producer's strength in the proximity network between each model phase. Changes between Phases 1 and 2 reflected the scroungers' social plasticity in response to the producer's added social value, while changes between Phase 3 and the other two phases indicated social plasticity, or the lack thereof, in response to the producer no longer having increased social value. To facilitate comparisons across group sizes, we scaled the producer’s strength by dividing it by the total group size before calculating differences in scaled strength between phases.

Identities saved in each agent’s sf-seen variable were used to understand the proportion of time that the scroungers had perceived the correct individual as the producer.

To understand the influence of each model parameter on the foraging success of scroungers, we calculated the median energy level achieved by scroungers at the end of each model run. Higher median energy reflected greater benefits received by scroungers as a result of following others (in simulations with asocial-information disabled) or a combination of following others and moving directly to food when it was available (in simulations with asocial-information enabled).

Investigating adaptive social plasticity

We explored whether different combinations of preference, memory, and attention values led to adaptive social plasticity in three contexts.

First, we investigated cognition and social plasticity. We determined whether changing the value one individual (the producer) provided to the group would change how group members interacted with it. We explored the parameter combinations facilitating this outcome by comparing the producer’s strength in Phase 2 to Phase 1. We predicted that, under parameter combinations allowing social plasticity, the change in value that the producer provided to the group, by being the sole individual able to open the food patch in Phase 2, would result in the other group members associating more with the producer. Therefore, the producer’s strength would increase in Phase 2 (when social value was gained) compared to initial conditions in Phase 1 (no added social value).

Second, we investigated cognition and the persistence of social changes. We determined whether any changes in associating with an individual who had become more valuable in the group persisted once that difference in value was removed. We compared the producer's strength in Phase 3 with its strength in Phase 2. We predicted that if changing the value of an individual resulted in a change in socializing with that individual, that taking away the producer's ability to differentially open the food would result in decreased strength, as others used social plasticity to return to previous levels of interaction.

Third, we explored whether any social changes could be considered adaptive. We determined whether parameter combinations associated with changes in the producer's strength were associated with the foraging success of other agents. To evaluate this, we compared the median energy value achieved by scroungers at the end of each simulation across parameter combinations. If social plasticity was adaptive, we predicted agents would have higher median energy values in simulations where they interacted more with the producer.

Sensitivity analysis

To understand the relationships between our model parameters and each outcome measure, we ran simulations across a wide parameter space. We ran the model 50 times for each of 1000 parameter combinations, where attention and preference each varied by increments of 0.25 (attention/preference = [0, 1]), memory varied by increments of 50 (memory = [0, 200]), group-size varied across four values (group-size = {3, 6, 10, 15}) and asocial-information was enabled or disabled.

If attention, preference, or memory was zero, foragers were only capable of making movements in random directions (when asocial-information was disabled) or directly toward an accessible food patch (when asocial-information was enabled). This allowed for comparisons of outcome measures to a baseline in each case within asocial-information conditions.

Following initial explorations of the model output, we used Generalized Additive Models (GAMs) built with the “mgcv” R package to more thoroughly explore the nonlinear relationships between cognitive parameters and each of three response variables for simulations with a group size of 15 and asocial-information enabled. We ran three separate GAMs in which the response variable was the change in producer’s strength from Phase 1 to Phase 2, the change in producer’s strength from Phase 2 to Phase 3, or the median energy level achieved by scroungers. The predictor in each GAM was a tensor product interaction term including attention, preference, and memory, which tested for the existence of combined nonlinear effects on the response variable. We assessed model validity using residual plots provided by the gam.check function from the mgcv package. For our model of the change in producer’s strength from Phase 1 to Phase 2, we added a constant to all values to make them positive and square root transformed the variable to improve normality and homoscedasticity. Model fits were compared using the Akaike Information Criterion (AIC).

Analyses were done in R version 4.1.0 (R Core Team 2021)

Results

Overall, we saw a clear influence of attention, preference, memory and asocial-information on both the magnitude of change in the producer's strength between phases and the foraging success of scroungers. Patterns were often qualitatively similar across group sizes and asocial-information conditions. We therefore present representative results for these parameters in some cases, but plots for all levels of these parameters are provided in Supplemental Information 1 (Figures S2, S3, S5, S6, S8 and S9).

Which combinations of cognitive skills enabled social plasticity?

We found that several parameter combinations resulted in an increase in producer strength from Phase 1 to Phase 2 when the producer became valuable due to gaining the ability to make food accessible. This was consistent with our prediction that producer strength would increase in Phase 2 compared to Phase 1 when agents had cognitive skills facilitating social plasticity. Non-zero values of all three parameters (attention, preference, and memory) were required for the producer to experience an increase in strength above a baseline produced by random movements alone or a combination of random movements and direct approaches toward food (Fig. 2). Increasing attention led to increased strength, but this increase was only seen up to attention values of 0.5, after which increasing attention had a negligible effect on strength (Fig. 3A). Increasing preference led to a more linear increase in strength with no plateau (Fig. 3B). For both attention and preference, similar patterns were seen in both the asocial-information enabled and disabled model runs, but with more of a plateau with increasing preference when asocial-information was disabled (Supplementary Figure S3). In contrast, changes in memory led to different responses when asocial-information was enabled versus disabled. When asocial-information was disabled, there was a larger increase in strength from memory 0 to 50, but it then plateaued (Fig. 3C). However, when asocial-information was enabled, short and long memory resulted in smaller changes in strength compared to intermediate values where we saw a peak increase in strength (Fig. 3C).

To examine the relationship between memory and the change in producer's strength from Phase 1 to Phase 2 in more detail, we determined the identity of the individual stored in each agent's memory. We found that the nonlinear effects of memory on strength were due to differences in whether the agents remembered the producer as the successful forager or had stored another individual in their memory. When asocial-information was enabled, intermediate values of memory were associated with the largest proportion of times agents stored the producer as the successful forager (Fig. 3D). When memory was greater than 100, the proportion of times agents stored the producer as the successful forager fell, reaching a median of zero for all group sizes when memory was 200 (Fig. 3D). This decrease for longer values of memory shows the drawbacks to longer but rigid memory in two ways. First, agents that stored the identity of a successful forager in Phase 1 who did not turn out to be the valuable individual in Phase 2 could not update their memories fast enough to exhibit adaptive social plasticity towards the producer. Second, agents could have identified the wrong individual as a successful forager even in Phase 2 if they failed to perceive the producer access the food but observed a scrounger at the food patch soon after. This was more likely to happen when asocial-information was enabled because scroungers were able to move directly to the food patch as soon as their energy decreased below a threshold and thus had a higher chance of being perceived feeding compared to simulations in which asocial-information was disabled.

Larger group sizes tended to result in larger increases in strength across memory, attention, and preference values (Fig. 3).

A Generalized Additive Model for a group size of 15 and asocial-information enabled confirmed a significant joint nonlinear relationship between our three cognitive parameters and the change in producer's strength from Phase 1 to Phase 2 (EDF = 63.23, F = 63.89, p < 0.001). Fitted lines reinforced our interpretations of the patterns between predictor and response variables (Supplementary Figure S4).

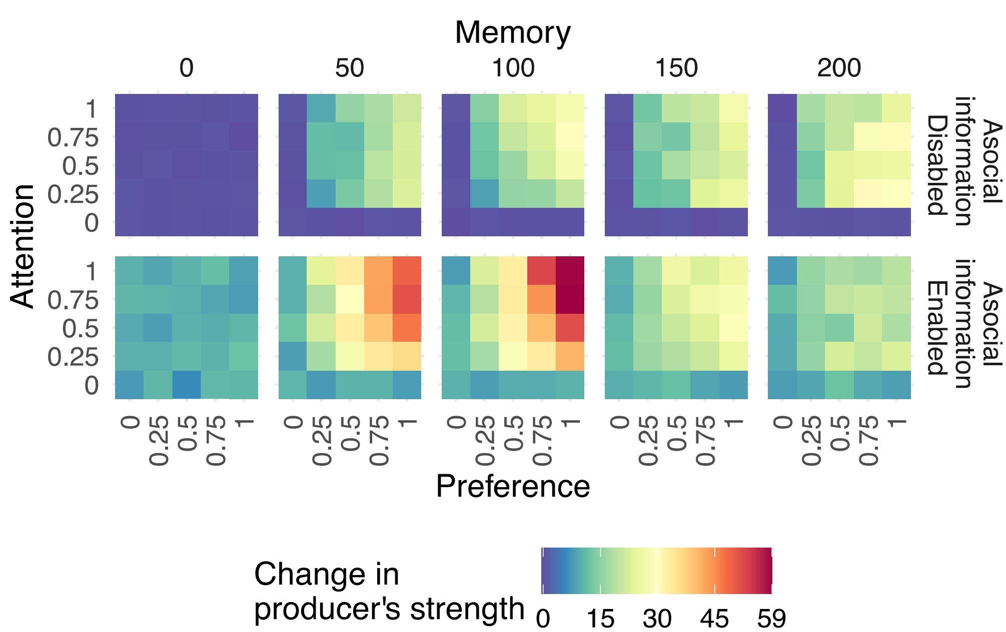

Figure 2. Median differences in the producer's strength (scaled by group size) between Phase 1 and Phase 2 for a group size of 15. Colors represent the magnitude and direction of change in strength from Phase 1 to Phase 2, either showing little to no change (dark blue), or an increase in strength (light blue through red) across 50 model runs.

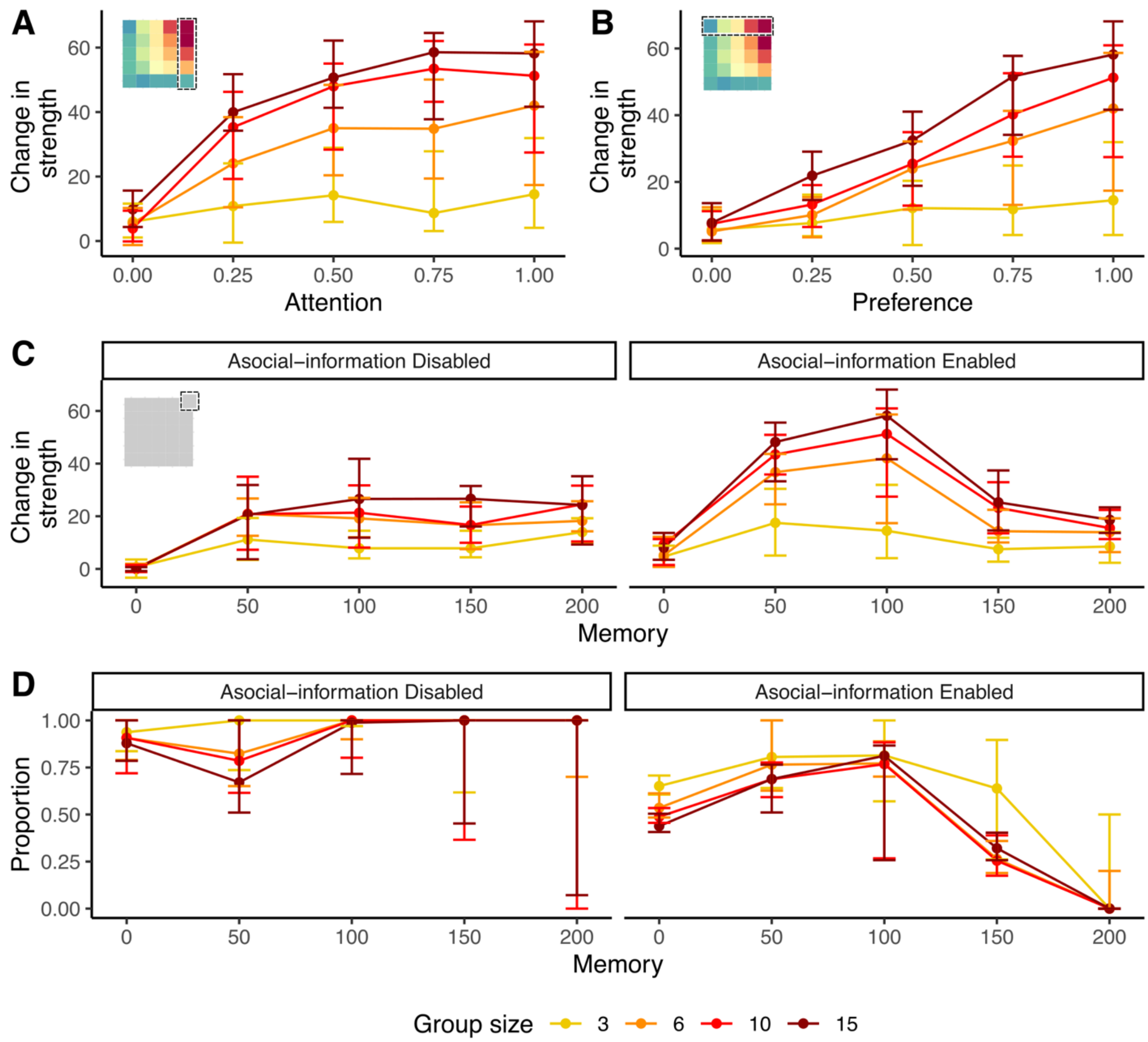

Figure 3. Median and interquartile range of the change in scaled strength between Phase 1 and Phase 2 from 50 model runs when **(A)** varying attention while keeping preference at 1 and memory at 100, **(B)** varying preference while keeping attention at 1 and memory at 100, and **(C)** varying memory while keeping attention and preference at 1. **(D)** median and interquartile range of the proportion of times within phase two that the producer is being remembered as a successful forager by scroungers. Insets outline the sections of heatmaps in Figure 2 that correspond to the variable plotted on the x-axis.

Which combinations of cognitive skills allowed initial plastic social responses to persist?

When we investigated whether changes in the producer's strength seen in Phase 2 persisted into Phase 3, we found results partly consistent with our predictions. Consistent with patterns we saw in the producer's strength between Phase 1 and Phase 2, increasing values of attention and preference at low to intermediate (50, 100) and high (200) values of memory were associated with larger changes, in this case decreases, in strength from Phase 2 to Phase 3 (Fig. 4 and Fig. 5 A-B). However, when memory was 150, the producer's strength sometimes increased in Phase 3 and larger increases occurred when asocial-information was enabled compared to when it was disabled (Fig. 5C). Once again, looking at the proportion of times agents stored the producer as the successful forager in their memory was informative. During Phase 3, this proportion was highest when memory was 150 (Fig. 5D). This suggests a memory of 150 was short enough for scroungers to forget whoever they remembered in Phase 1 but long enough to remember the producer in Phase 2 through Phase 3. In effect, this created a lag between when the producer's role of making food accessible was active and when the scroungers chose to follow it. A memory of 200 in comparison may have prevented scroungers from changing who was in their memory in Phase 2, effectively preventing them from perceiving the producer's increase in social value at all.

Similar to our previous analysis, a Generalized Additive Model on data from simulations with a group size of 15 and asocial-information enabled confirmed a significant nonlinear relationship between our three cognitive parameters and the change in producer's strength from Phase 2 to Phase 3 (EDF = 56.19, $F = 74.05$, $p < 0.001$). Fitted lines reinforced our interpretations of the patterns between predictor and response variables (Supplementary Figure S7).

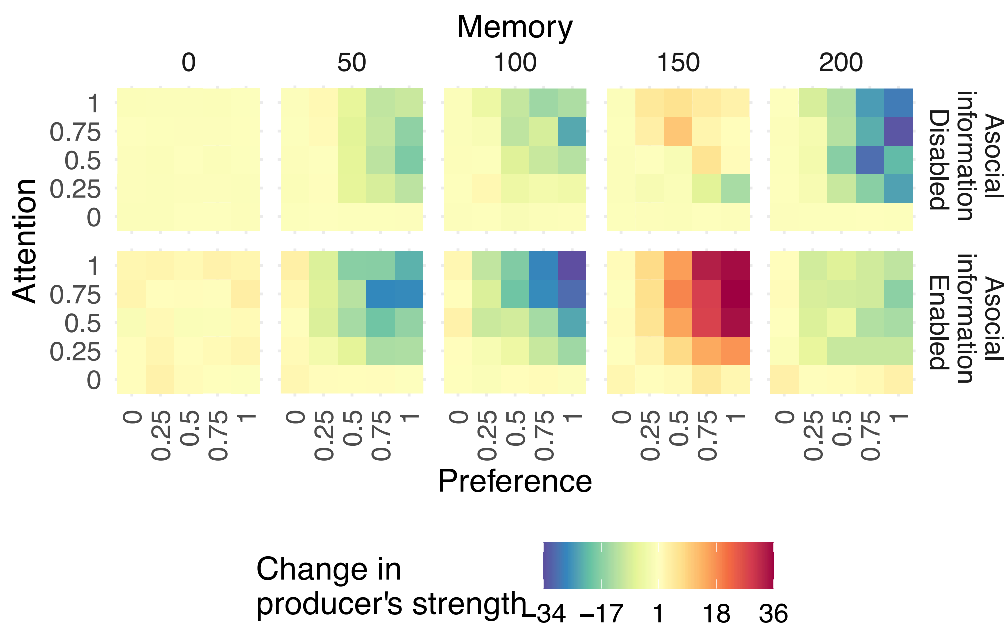

Figure 4. Median differences in the producer's strength (scaled by group size) between Phase 2 and Phase 3 for a group size of 15. Colors represent the magnitude and direction of change in strength from Phase 2 to Phase 3, either showing a decrease (dark blue through light blue), little to no change (teal) or an increase in strength (yellow through red) across 50 model runs.

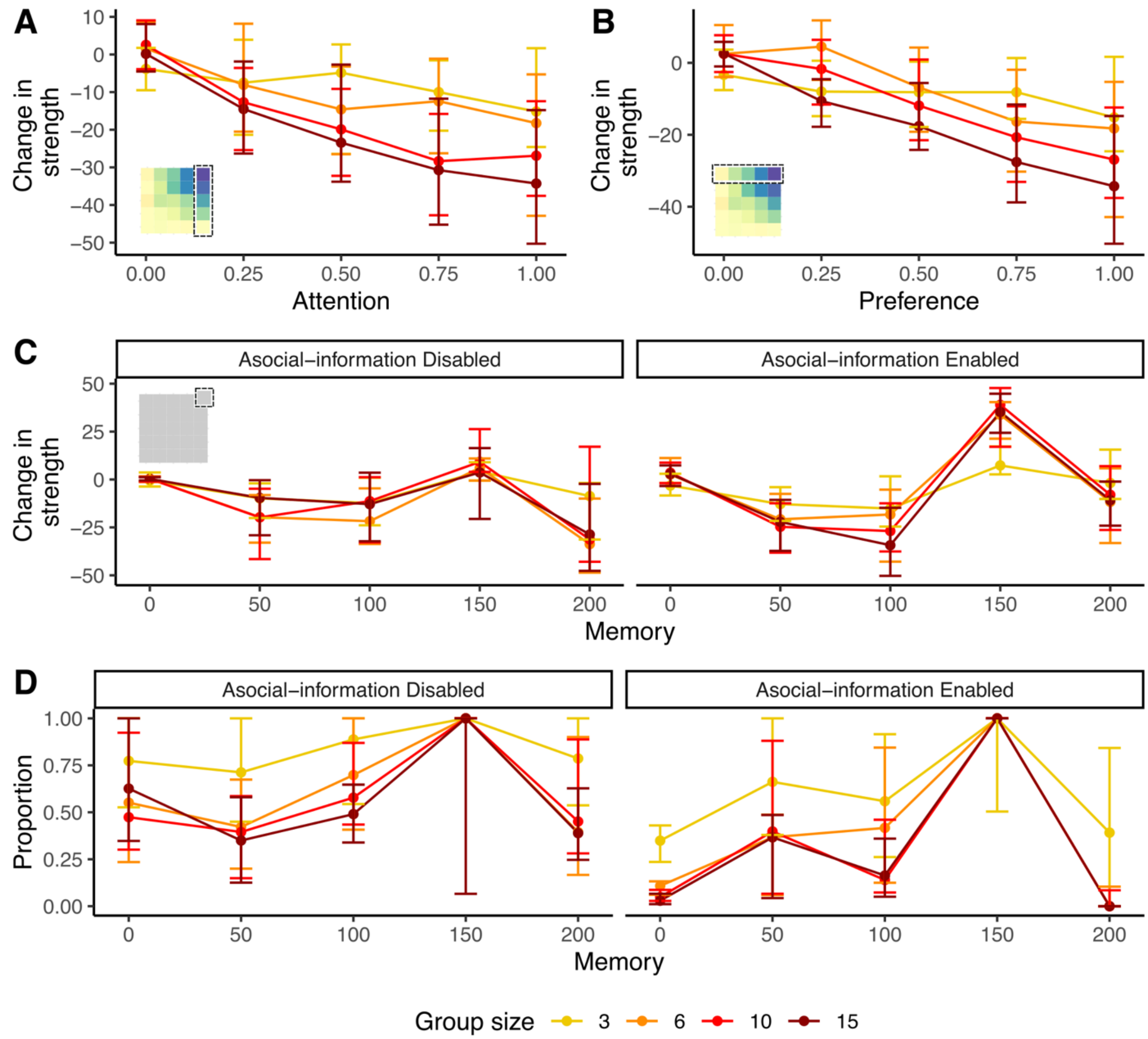

Figure 5. Median and interquartile range of the change in scaled strength between Phase 2 and Phase 3 when varying **(A)** attention while keeping preference at 1 and memory at 100, **(B)** preference while keeping attention at 1 and memory at 100, and **(C)** memory while keeping attention and preference at 1. **(D)** median and interquartile range of the proportion of times within phase three that the producer is being remembered as a successful forager by scroungers. Insets outline the sections of heatmaps that correspond to the variable plotted on the x-axis.

Did social plasticity provide benefits to scroungers?

When examining the conditions in which scroungers benefited the most from their following decisions, we found evidence that conflicted with our prediction. Agents generally achieved a greater median energy when asocial-information was enabled compared to when it was disabled (Fig. 6). When asocial-information was enabled, our initial exploration of the data showed the median energy of scroungers tended to remain stable or decrease slightly with increasing attention (Fig. 7A) and memory (Fig. 7C). Low to intermediate values of preference were associated with the highest median energy values (Fig. 7B). Finally, larger group sizes were associated with lower median energy levels (Fig. 7), reflecting greater competition for resources in larger groups.

Our Generalized Additive Model with median scrounger energy as the response variable showed a significant synergistic effect of the cognitive parameters ($EDF = 86.6$, $F = 27.11$, $p < 0.001$). Visualizations of the effects revealed more complex relationships than our initial exploration. Median scrounger energy increased or decreased with increasing attention values depending on the value of the preference parameter (Fig. 8A). Our previous recognition of a peak in median energy occurring at low to intermediate values of preference was a consistent pattern across parameter combinations (Fig. 8B). There was a nonlinear relationship between memory and scrounger energy, which was also influenced by attention and preference values. Additionally, there was a consistent dip in energy when memory was 150 time steps long (Fig. 8C). This dip likely relates to the lag between when the producer provided value in Phase 2 and when the scroungers chose to follow it in Phase 3, leading to missed foraging opportunities.

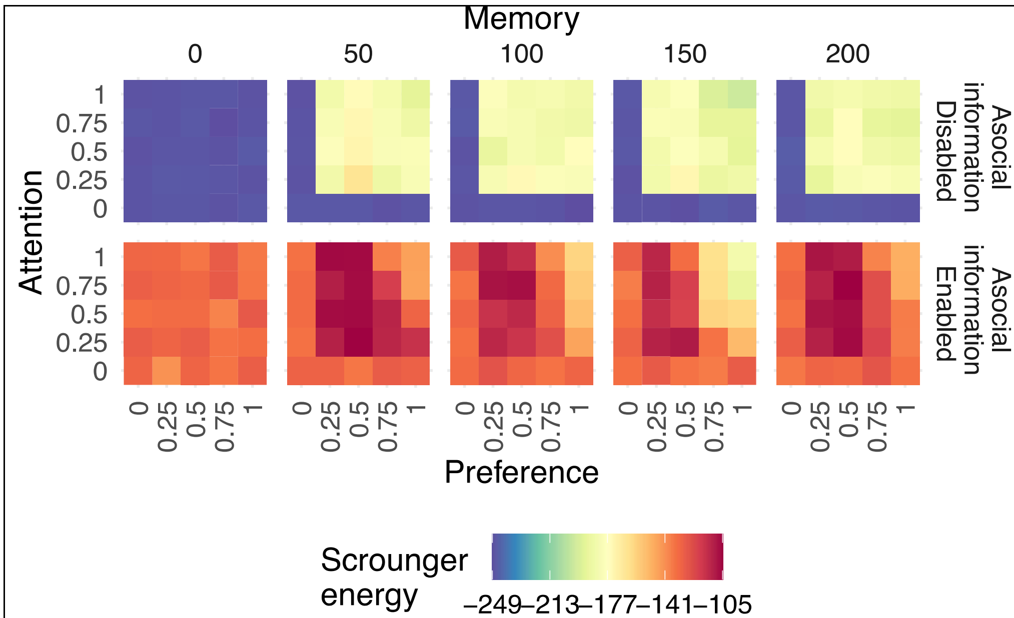

Figure 6. Median energy achieved by scroungers at end of simulations across 50 model runs for a group size of 15. The color scale reflects a range from low foraging success (dark blue) to high foraging success (red).

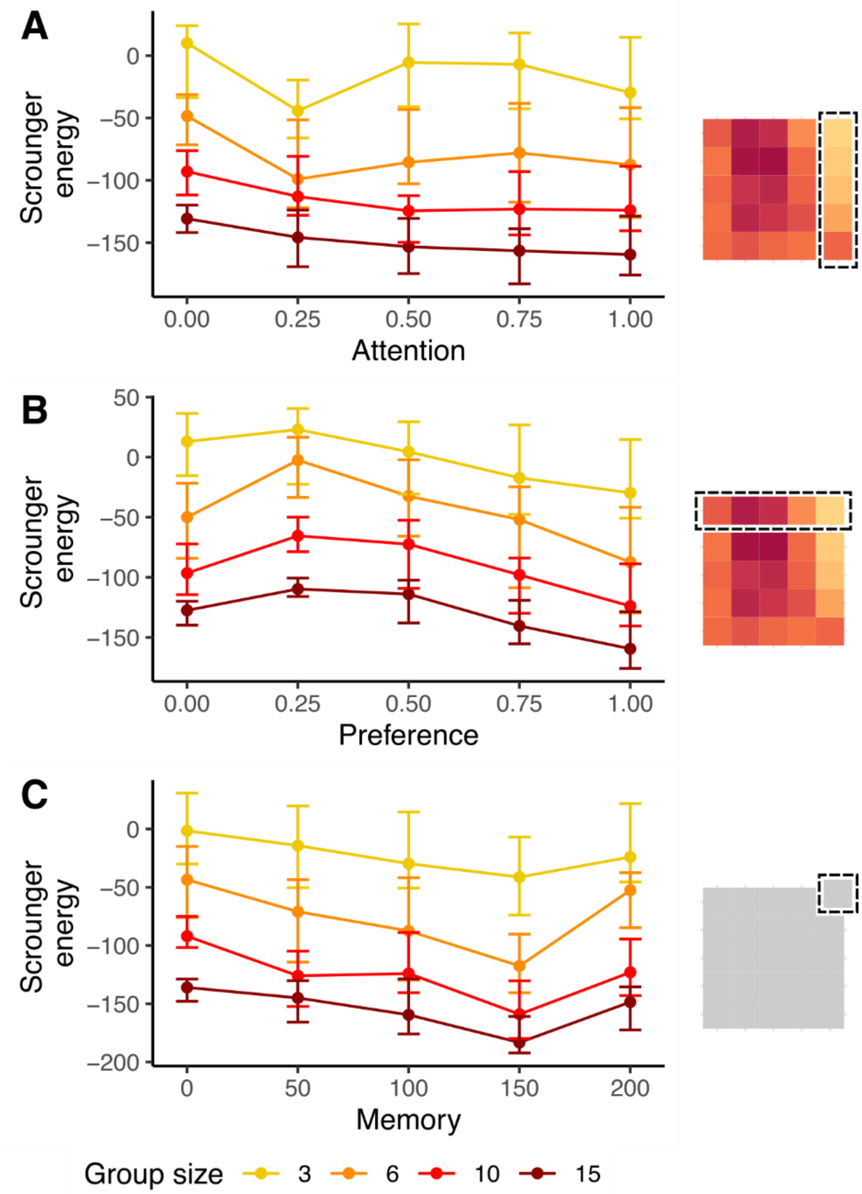

Figure 7. Median and interquartile range of the median energy achieved by scroungers when varying **(A)** attention while keeping preference at 1 and memory at 100, **(B)** preference while keeping attention at 1 and memory at 100, and **(C)** memory while keeping attention and preference at 1. Insets outline the sections of heatmaps in Figure 6 that correspond to the variable plotted on the x-axis. All plots show data from simulations with asocial-information enabled.

399

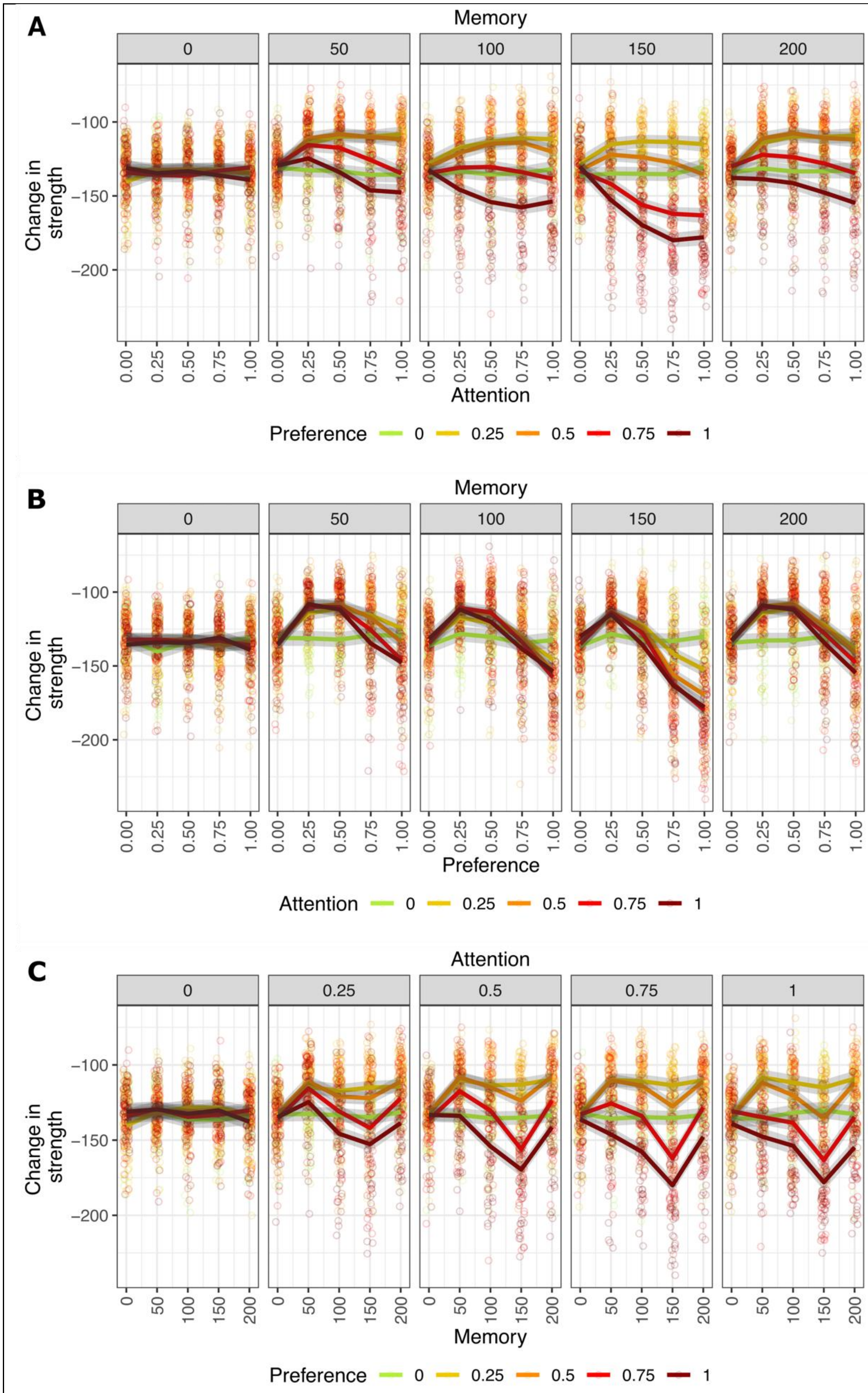
A
Memory
0
50
100
150
200
Change in strength
−100
−150
−200
0.00
0.25
0.50
0.75
1.00
Attention
Preference
0
0.25
0.5
0.75
1
B
Memory
0
50
100
150
200
Change in strength
−100
−150
−200
0.00
0.25
0.50
0.75
1.00
Preference
Attention
0
0.25
0.5
0.75
1
C
Attention
0
0.25
0.5
0.75
1
Change in strength
−100
−150
−200
0
50
100
150
200
Memory
Preference
0
0.25
0.5
0.75
1

Figure 8. The tensor-product smooth functions for (A) attention, (B) preference, and (C) memory, showing synergistic nonlinear effects on the median energy achieved by scroungers. Shaded areas represent the 95% confidence interval. Only data from simulations with a group size of 15 and asocial-information enabled are shown.

Discussion

Animals may adjust their social interactions to decrease the costs or increase the benefits they experience from their relationships, but the cognitive skills required for such adaptive social plasticity have not been studied directly. We built an agent-based model to investigate the cognitive skills necessary for adaptive social plasticity in a foraging context. We asked what combinations of cognitive skills were associated with plastic social responses to the producer's increased social value, which were associated with the persistence of these initial social responses, and which were associated with greater foraging success for scroungers. Overall, we found evidence partly in line with our predictions, but some results relating to the effect of memory were unexpected.

Cognitive skills enabling social plasticity

We first asked what combination of cognitive parameters lead to increases in the producer's strength in the group's proximity network when its social value is increased. As expected, all three cognitive parameters were necessary to see plastic responses to the producer's change in value. Furthermore, parameter combinations that facilitated following successful foragers led to stronger plastic responses. The producer’s strength increased in Phase 2 under high attention and preference values and short to intermediate memory.

Our findings that the producer’s strength increased in Phase 2 under some conditions are in line with those of multiple empirical studies, supporting our view that the cognitive parameters we modeled may be relevant in the real-world. Fruteau et al. (2009) and Kulahci et al. (2018) both observed increased grooming rates experienced by individual primates that successfully opened novel foraging tasks. Birds have also been shown to increase their social associations with individuals that seemingly provided more reliable information about food location or that facilitated access to a feeder (Firth et al. 2016; Heinen et al. 2022; Kings et al. 2023). Similarly, Romero-González et al. (2020) showed that bumblebees (*Bombus terrestris*) learned the reward-predictive value of conspecifics and later chose to be in closer proximity to a live demonstrator that matched the phenotype of the previously reward-predicting conspecific models. To facilitate a deeper understanding of the cognition underlying the adaptive social plasticity exhibited in each of these systems, our model may be modified to more closely resemble each system and parameterized with real-world metrics like interaction rates.

Our findings also resemble models of group formation or cooperation. Cantor and Farine (2018) showed that subgroupings of individuals can emerge if individuals choose to continue foraging with their most recent foraging partners if they were able to find enough food. Similarly, models of cooperation show it can be favored when individuals have control over who they interact (Santos et al. 2006; Aktipis 2011). These similarities emphasize the potential broad implications of adaptive social plasticity. The ability to perceive and adaptively respond to the benefits provided by group members may impact group structure and the development of trusted relationships. Our model can therefore adapted to provide a look at the cognition underlying these broader social outcomes.

Cognitive skills allowing persistence of initial plastic social responses

Our second research question focused on the persistence of scroungers' initial responses to the producer's added social value. We asked what parameters allowed changes in the producer's strength to persist when it no longer had the sole ability to make the food patch accessible. Here the producer's strength largely decreased under the same conditions as it had increased in Phase 2. Unexpectedly, there was a lag effect when memory was 150 causing agents to follow the producer more in Phase 3 compared to Phase 2, so the producer's strength increased in the final phase. Constraints in our model dynamics, specifically that agents could only remember one successful forager at a time and only update it after enough time steps had passed, prevented a simpler pattern of longer persistence of the producer's change in strength with longer memory from emerging.

Cognitive skills facilitating greater foraging success for scroungers

Our third research question focused on whether the social responses exhibited by scroungers benefitted them. We asked what parameter combinations were associated with greater foraging success for scroungers. Preference had a strong influence, with low to intermediate preference values associated with the highest energy levels for scroungers at the end of a simulation. Overall, agents benefitted the most from a strategy in which they only occasionally followed successful foragers and could more frequently update the successful forager in their memory.

It has been theorized that the use of social information should be favored when environmental conditions are changing, but not too rapidly (Stephens 1991; Kendal et al. 2005; Aoki and Feldman 2014). If the environment is very volatile, social information may quickly become outdated. Indeed, multiple models have shown that selective use of social information can prevent costly foraging decisions (Garg et al. 2022) and be favored when environments or resources are fluctuating to some degree (McElreath et al. 2005; Smolla et al. 2015; Gilman et al. 2020). In our model, the main environmental change involved food accessibility, where the food patch was first accessible to all agents, then to the producer alone, and then to all agents again. A flexible use of social information in this context, exhibited at low to intermediate preference values, proved to be beneficial as agents could forage on their own in Phases 1 and 3, but also take advantage of the producer's foraging behavior in Phase 2. In contrast, a more strict adherence to following successful foragers was less beneficial due to the uncertainty about who the true producer was in Phase 1 (especially when asocial-information was enabled) and the inability of agents who remembered the wrong individual to correct their mistake in Phase 2. Our findings therefore reflect the existence of an optimal cognitive flexibility that allows agents to take advantage of knowledgeable individuals in the group without being stuck with outdated or inaccurate information.

Our model provides a general representation of a foraging group of animals undergoing a single foraging event. Adding feedback between the foraging success of scroungers and their choice to follow other agents over consecutive foraging bouts would provide a more direct illustration of how evaluations of social value, and flexibility in the use of social information, influence social dynamics. A model of social dynamics could incorporate an explicit learning process, such as the linear operator learning rule (Beauchamp 2000; Katsnelson et al. 2012; Afshar and Giraldeau 2014) or Bayesian updating (Aubier and Kokko 2022; Perkes and Laskowski 2023), with which agents decide to associate with other individuals based on the foraging success they experienced from associating with those individuals in the past. Incorporating learning would have the added benefit of preventing potential artifacts with respect to the effect of memory on changes in social connectedness, which arose in our current model from limitations in the number of agents an individual could remember.

Model limitations and potential future directions

We have shown that the cognitive abilities modeled here can lead to changes in social relationships that could be beneficial for both the producer and scroungers. However, agent-based models are usually simpler than real empirical systems and simplifying assumptions often must be made. In our model, one major simplifying assumption we made is that memory for successful foragers is rigid and unchanging over our memory timescales. In real systems, memory for particular individuals is likely to be less rigid, but in many animal species, we lack empirical evidence for memory formation and function. Relaxing this assumption could lead to different dynamics, which could be explored in future modeling work. In our model we also did not explicitly model the benefits that the producer might receive from achieving greater social connectedness. We are assuming that greater strength in a proximity network would be beneficial for the producer based on findings from empirical research (e.g., increased survival rates for more connected individuals, Cheney et al. 2016). Social network dynamics are often also influenced by costs, such as increased risk of disease transmission (Lopes et al. 2016; Stroeymeyt et al. 2018; Ripperger et al. 2020; Romano et al. 2020), which should be incorporated into future models. In addition, we modeled a single valuable producer and a single food patch. Inclusion of multiple producers and/or multiple patches would create a more complex social landscape that could be used to test whether cognitive parameters like attention, preference, and memory, could lead to social patterns predicted under biological market theory (Noë and Hammerstein 1995; Fruteau et al. 2009). Finally, we modeled a scenario without previous social histories or preexisting relationships among individuals. These might be important as some animals have been shown to forgo foraging opportunities that would separate them from their close associates (Firth et al. 2015; Kings et al. 2023). Including pre-existing associations would allow for the exploration of the trade-off between managing long-term relationships and short-term adaptive social plasticity.

Conclusion

Using an agent-based model we showed that simple cognitive skills allow for potentially mutually beneficial changes in social relationships for producers and scroungers. Strong tendencies for scroungers to perceive and follow successful foragers led to large increases in the producer's strength in a proximity network and the timing and magnitude of these increases was strongly influenced by memory. In comparison, weak tendencies for following successful foragers were associated with the best foraging success for scroungers. Given the ecological importance of foraging for wild animals, studying social foraging scenarios is a high priority for understanding social cognition. Foraging experiments allow researchers to tease apart the social and environmental factors responsible for social plasticity and these experiments provides a structure that can inspire agent-based models designed with the most critical factors in mind. Models may be built to closely match the dynamics of specific study systems to facilitate more direct comparisons between computational and empirical results. Future computational and empirical work on adaptive social plasticity could provide a deeper understanding of the cognition underlying this process.

Funding

This work was supported by the National Science Foundation [NSF IOS 1016190 to EAH]; the University of Cincinnati's Graduate College Dean's Fellowship to SP; and a Grant in Aid of Research from Sigma Xi, The Scientific Research Society [G20201001116641584 to SP]

Acknowledgements

We thank Alejandro Perez Velilla and Vanessa Ferdinand for helpful discussions and Neeltje Boogert for comments on an early draft of the paper.

References

Afshar M, Giraldeau L-A. 2014. A unified modelling approach for producer–scrounger games in complex ecological conditions. Anim Behav 96:167–76.

Afshar M, Hall CL, Giraldeau LA. 2015. Zebra finches scrounge more when patches vary in quality: Experimental support of the linear operator learning rule. Anim Behav 105:181–86.

Aktipis CA. 2011. Is cooperation viable in mobile organisms? Simple Walk Away rule favors the evolution of cooperation in groups. Evol Hum Behav 32:263–76.

Aoki K, Feldman MW. 2014. Evolution of learning strategies in temporally and spatially variable environments: A review of theory. Theor Popul Biol 91:3–19.

Aubier TG, Kokko H. 2022. Volatile social environments can favour investments in quality over quantity of social relationships. Proc R Soc B 289:20220281.

Barnard CJ, Sibly RM. 1981. Producers and scroungers: A general model and its application to captive flocks of house sparrows. Anim Behav 29:543–50.

Beauchamp G. 2000. Learning Rules for Social Foragers: Implications for the Producer–Scrounger Game and Ideal Free Distribution Theory. J Theor Biol 207:21–35.

Blersch R, Vandeleest JJ, Nathman AC, Pósfai M, D'Souza R, McCowan B, Beisner BA. 2024. What you have, not who you know: food-enhanced social capital and changes in social behavioural relationships in a non-human primate. R Soc Open Sci 11:231460.

Cantor M, Farine DR. 2018. Simple foraging rules in competitive environments can generate socially structured populations. Ecol Evol 8:4978–91.

Cantor M, Maldonado-Chaparro AA, Beck KB, Brandl HB, Carter GG, He P, Hillemann F, Klarevas-Irby JA, Ogino M, Papageorgiou D, Prox L, Farine DR. 2021. The importance of individual-to-society feedbacks in animal ecology and evolution. J Anim Ecol 90:27–44.

Cheney DL, Silk JB, Seyfarth RM. 2016. Network connections, dyadic bonds and fitness in wild female baboons. Royal Society Open Science 3:160255.

Dubois F, Morand-Ferron J, Giraldeau L-A. 2010. Learning in a game context: strategy choice by some keeps learning from evolving in others. Proc R Soc B 277:3609–16.

Firth JA, Sheldon BC, Farine DR. 2016. Pathways of information transmission among wild songbirds follow experimentally imposed changes in social foraging structure. Biol Lett 12:20160144.

Firth JA, Voelkl B, Farine DR, Sheldon BC. 2015. Experimental Evidence that Social Relationships Determine Individual Foraging Behavior. Curr Biol 25:3138–43.

Fruteau C, Voelkl B, Van Damme E, Noë R. 2009. Supply and demand determine the market value of food providers in wild vervet monkeys. Proc Natl Acad Sci 106:12007–12.

Garg K, Kello CT, Smaldino PE. 2022. Individual exploration and selective social learning: balancing exploration–exploitation trade-offs in collective foraging. J R Soc Interface 19:20210915.

Gilman RT, Johnson F, Smolla M. 2020. Competition for resources can promote the divergence of social learning phenotypes. Proc R Soc B 287:20192770.

Grimm V, Berger U, Bastiansen F, Eliassen S, Ginot V, Giske J, Goss-Custard J, Grand T, Heinz SK, Huse G, Huth A, Jepsen JU, Jørgensen C, Mooij WM, Müller B, Pe'er G, Piou C, Railsback SF, Robbins AM, Robbins MM, Rossmanith E, Rüger N, Strand E, Souissi S, Stillman RA, Vabø R, Visser U, DeAngelis DL. 2006. A standard protocol for describing individual-based and agent-based models. Ecological Modelling 198:115–26.

Grimm V, Railsback SF, Vincenot CE, Berger U, Gallagher C, Deangelis DL, Edmonds B, Ge J, Giske J, Groeneveld J, Johnston ASA, Milles A, Nabe-Nielsen J, Polhill JG, Radchuk V, Rohwäder MS, Stillman RA, Thiele JC, Ayllón D. 2020. The ODD protocol for describing agent-based and other simulation models: A second update to improve clarity, replication, and structural realism. Jasss 23.

Heinen VK, Benedict LM, Sonnenberg BR, Bridge ES, Farine DR, Pravosudov VV. 2022. Experimental manipulation of food distribution alters social networks and information transmission across environments in a food-caching bird. Anim Behav 193:1–12.

Hobson EA, DeDeo S. 2015. Social Feedback and the Emergence of Rank in Animal Society. PLoS Comput Biol 11:e1004411.

Hobson EA, Ferdinand V, Kolchinsky A, Garland J. 2019. Rethinking animal social complexity measures with the help of complex systems concepts. Anim Behav 155:287–96.

Hobson EA, Mønster D, Dedeo S, Strassmann JE. 2021. Aggression heuristics underlie animal dominance hierarchies and provide evidence of group-level social information. Proc Natl Acad Sci 118:e2022912118.

Katsnelson E, Motro U, Feldman MW, Lotem A. 2012. Evolution of learned strategy choice in a frequency-dependent game. Proc R Soc B 279:1176–84.

Kendal RL, Coolen I, Van Bergen Y, Laland KN. 2005. Trade-Offs in the Adaptive Use of Social and Asocial Learning. Adv Stud Behav 35:333–79.

Kings M, Arbon JJ, McIvor GE, Whitaker M, Radford AN, Lerner J, Thornton A. 2023. Wild jackdaws can selectively adjust their social associations while preserving valuable long-term relationships. Nat Commun 14:5103.

Kulahci IG, Ghazanfar AA, Rubenstein DI. 2018. Knowledgeable Lemurs Become More Central in Social Networks. Curr Biol 28:1306–10.

Kulahci IG, Quinn JL. 2019. Dynamic Relationships between Information Transmission and Social Connections. Trends Ecol Evol 34:545–54.

Laland KN. 2004. Social Learning Strategies. Learn Behav 32:4–14.

Lopes PC, Block P, König B. 2016. Infection-induced behavioural changes reduce connectivity and the potential for disease spread in wild mice contact networks. Sci Rep 6:31790.

McElreath R, Lubell M, Richerson PJ, Waring TM, Baum W, Edsten E, Efferson C, Paciotti B. 2005. Applying evolutionary models to the laboratory study of social learning. Evol Hum Behav 26:483–508.

Morand-Ferron J, Giraldeau LA. 2010. Learning behaviorally stable solutions to producer-scrounger games. Behav Ecol 21:343–48.

Noë R, Hammerstein P. 1995. Biological markets. Trends Ecol Evol 10:336–39.

Perkes A, Laskowski K. 2023. Bayesian updating for self-assessment explains social dominance and winner-loser effects. .

R Core Team. 2021. R: A language and environment for statistical computing. .

Reichert MS, Morand-Ferron J, Kulahci IG, Firth JA, Davidson GL, Crofts SJ, Quinn JL. 2021. Cognition and covariance in the producer–scrounger game. J Anim Ecol 90:2497–2509.

Ripperger SP, Stockmaier S, Carter GG. 2020. Tracking sickness effects on social encounters via continuous proximity sensing in wild vampire bats. Behav Ecol 31:1296–1302.

Romano V, MacIntosh AJJ, Sueur C. 2020. Stemming the Flow: Information, Infection, and Social Evolution. Trends Ecol Evol 35:849–53.

Romero-González JE, Royka AL, MaBouDi H, Solvi C, Seppänen J-T, Loukola OJ. 2020. Foraging Bumblebees Selectively Attend to Other Types of Bees Based on Their Reward-Predictive Value. Insects 11:800.

Santos FC, Pacheco JM, Lenaerts T. 2006. Cooperation Prevails When Individuals Adjust Their Social Ties. PLoS Comput Biol 2:e140.

Smolla M, Gilman RT, Galla T, Shultz S. 2015. Competition for resources can explain patterns of social and individual learning in nature. Proc R Soc B 282:20151405.

Stephens DW. 1991. Change, regularity, and value in the evolution of animal learning. Behav Ecol 2:77–89.

Stroeymeyt N, Grasse AV, Crespi A, Mersch DP, Cremer S, Keller L. 2018. Social network plasticity decreases disease transmission in a eusocial insect. Science 362:941–45.

Wascher CAF, Kulahci IG, Langley EJG, Shaw RC. 2018. How does cognition shape social relationships? Phil Trans R Soc B 373:20170293.

Wilensky U. 1999. Netlogo.

Supplemental information 1

Overview, Design concepts and Details

Purpose.

The model was built to facilitate a deeper understanding of the cognition necessary for adaptive social plasticity. We model three cognitive parameters and analyze their influences on changes in a valuable agent's connectivity in a social network and the foraging success of the group.

Entities, State Variables, and Scales.

The model has four kinds of entities: a producer, scroungers, a food patch, and the observer (global environment). In each simulation there is always a single producer, which is the agent that receives a foraging advantage in Phase 2 of each model run. Scroungers are all agents other than the producer and the number of scroungers varies between 2 and 14. All agents have three state variables: *energy*, *sf-seen*, and *sf-seen-timer*. Energy denotes the energy level of the agent, sf-seen stores the identity of the agent who was perceived feeding, and sf-seen-timer tracks the number of time steps that have passed since an identity was entered in the sf-seen variable. Note that the sf-seen and sf-seen-timer variables do not influence the movement decisions of the producer. The four central grid cells in the model space together form a single square food patch. Each food patch grid cell has a resource-level variable that tracks the resources available, and a reset-counter variable that tracks the number of time steps that have passed since the food patch was depleted. Additionally, the accessibility status of the food patch is determined by its color (black = inaccessible to all agents, yellow = accessible to the producer, and green = accessible to all agents). Finally, the observer tracks global variables (Table 1) that were used either to control submodels or to store data to be used for analyses in R.

The model represents a group of animals foraging in a closed arena. The spatial scale of the model varies with group size between a 15 by 15 cell arena for a group size of 3 and a 31 by 31 cell arena for a group size of 15. Each simulation proceeds for a total of 300 time steps representing a single continuous foraging period.

Table 1. Global variables and their meanings. Variables used for model dynamics are shown in bold text.

Variable name	Meaning
current-succ-foragers	List holding identities of successful foragers in each time step – updated at each time step

prox-centrality-list	List of integers representing the number of other agents in proximity to each individual – updated at each time step
proxim-IDs	List containing lists of identities of agents in proximity to each individual – updated at each time step
fss-list	List containing the sf-seen value of each individual – updated at each time step
energy-list	List containing the energy level of each individual – updated at each time step
deplete-num	Number of times the food patch was depleted during the first and third model phases
reset-num-for	Number of times the food patch was reset during the second model phase
deplete-count	Tracks number of time steps passed since the food patch was depleted in the first and third model phases

Process Overview and Scheduling.

After initialization, the model proceeds in three phases. In each phase, the agents make movement decisions influenced by the global parameters attention, preference, memory and asocial-information. In Phases 1 and 3, the food patch is accessible to all agents, but in Phase 2 the food patch must be accessed by the producer before it can be accessed by any scrounger. The scheduling of the phases within each simulation allows for the determination of baseline proximity relationships (Phase 1), how the producer's proximity relationships change when it has a foraging advantage (Phase 2), and whether any changes in the producer's proximity relationships persist when it no longer has a foraging advantage (Phase 3).

The same actions are executed at each time step no matter which phase of the simulation is ongoing. First, the observer resets the current-succ-foragers variable so that it is an empty list. Next, the producer decides whether to feed, move toward the food patch, or move in a random direction and updates the global variables current-succ-foragers and energy-list accordingly. Each scrounger then takes a turn, in a random order, deciding whether to feed, move toward the food patch, move toward the agent stored in its sf-seen variable, or move in a random direction. Scroungers also update the current-succ-foragers list and energy-list as appropriate.

Decisions to feed increase the acting agent's energy level while decreasing the food patch's resource-level.

After all agents have made their foraging/movement decisions, the deplete-count variable is increased by one if the food patch as a whole was depleted below a certain threshold resource-level. If the current-succ-foragers list was updated by any agent, all agents run a procedure to determine whether they will update their sf-seen variable. Finally, procedures to update the fss-list, prox-centrality-list, and proxim-IDs variables are executed.

Design Concepts.

Our model was designed to resemble empirical experiments that have investigated how changes to the value of group members lead to changes in social interactions received by those group members (Kulahci et al. 2018; Blersch et al. 2024). In such experiments, the value of a group member is manipulated by giving it special access to a food source (a novel foraging task or automated feeder).

The basic principle behind this model is the hypothesis that cognitive skills influence animals' ability to exhibit adaptive social plasticity. We model attention, preference, and memory as cognitive parameters to understand how they influence the emergence of adaptive social plasticity in a foraging context. Attention is the probability with which agents perceive others that successfully foraged in a time step (and save the identity of one of those individuals in their sf-seen variable). Varying values of attention in our model are meant to reflect varying levels of perception or ability to sense the foraging activity of others (either as a result of underlying cognitive capacity, external environmental conditions, or varying underlying reliance on social information). Preference is the probability with which agents follow the individual they perceived as a successful forager and reflects a decision-making process. Varying values of preference are meant to represent differences in the value placed on social information that is perceived. Finally, memory is the number of time steps that agents store an individual in their sf-seen variable. Agents are not able to update their sf-seen variable until it resets after a number of time steps equal to the memory value have passed.

Proximity relationships between agents (and therefore the producer's strength in the proximity network) and their final energy levels emerge as a result of the movement decisions of agents.

The main source of stochasticity in the model comes from the movement of agents in a randomly chosen direction when they decide not to execute any other movement or foraging options. Incorporating such stochasticity is meant to represent noise in proximity relationships.

Model outcomes are extracted by having agents update global variables tracking proximity relationships and energy levels at each time step.

Initialization.

At initialization, the arena is resized according to the total number of individuals in the group (set by the group-size parameter), such that spatial density is kept constant across group sizes. One producer and a number of foragers (group-size - 1) are created and each receives an initial energy value drawn from a normal distribution with a mean of 50 and standard deviation of 10 (this mean and standard deviation are constant across all simulations). Each agent starts with an empty sf-seen variable and a sf-seen-timer value of zero. Each agent is moved to a randomly selected empty patch in the arena. Next, the global variables are created as empty lists or with values of zero (for deplete-num, reset-num-for, and deplete-count). The initial energy values of agents are entered into the energy-list variable. Lastly, the food patch is created with an initial resource value of 400 (100 for each of the four cells that make up the food patch) and a reset-counter value of zero.

Input Data.

The model does not use input data to represent time-varying processes.

Submodels.

The following processes occur at each time step within a simulation.

Producer foraging and movement actions

The producer takes one step in a random direction if its energy level is above a fixed threshold (50). It feeds (i.e., increases its energy level by 10 while simultaneously decreasing the resource level of the food patch by the same amount) when it is on the food patch and its energy level has dropped below the threshold. If it is not on a food patch and its energy level drops below a lower fixed threshold (30), it takes a step directly toward the food patch. In Phase 2 of each simulation, the food patch becomes accessible to all agents (it turns green) when the producer feeds. Producer movements are not influenced by the global parameters attention, preference, memory, and asocial-information.

At the end of the producer's turn it adds its own ID number to the current-succ-foragers list if it fed in that time step, decreases its energy-level by one, and adds its new energy-level to the energy-list variable.

Scrounger foraging and movement actions

Each scrounger first increases its sf-seen-timer by 1 if there is an agent ID saved in its sf-seen variable. If the sf-seen-timer value exceeds the value of the *memory* parameter, that scrounger's sf-seen variable is erased, and it may remember a new agent in the future. Next, like the producer, the scrounger will take an action depending on its energy level and whether it is on the food patch. It feeds if its energy is below a threshold (50) and it is on the food patch when the food is accessible to non-producers. When *asocial-information* is enabled, the agent will move directly toward the accessible food patch if its energy is below the lower threshold (30). When asocial-information is disabled, agents are not able to move directly toward the food patch and their movement is only influenced by the other three parameters mentioned above (scroungers may still stumble upon the food patch and feed). Whether asocial-information is enabled or not, scroungers run the “movement” procedure if their energy is above the high threshold (50), or the food patch is not currently accessible to them. Within the “movement” procedure, foragers draw a random number from 0 to 1 to determine whether they will follow the agent saved in their sf-seen variable. If the random number is below the value of the *preference* parameter, the scrounger takes a step toward its sf-seen. Scroungers whose sf-seen variable is empty, or that drew a number lower than *preference*, take a step in a random direction.

At the end of a scroungers turn it adds its own ID number to the current-succ-foragers list if it fed in that time step, decreases its energy-level by one, and adds its new energy-level to the energy-list variable.

<u>Updating sf-seen</u>

A procedure for updating each agent’s sf-seen variable is run if there was at least one agent that fed in the current time step. Scroungers that do not have an agent ID saved in their sf-seen variable draw a random number from 0 to 1 to determine whether they perceived one of the successful foragers. If the random number is below the value of the attention parameter, the forager saves the ID of the successful forager in its sf-seen variable. If there were multiple successful foragers in the current time step, the ID of one of them is chosen at random to be saved in the sf-seen variable. If the random number drawn by the agent is equal to or greater than the value of attention, its sf-seen variable remains empty.

<u>Depleting and resetting the food patch</u>

In Phases 1 and 3, the food patch is depleted when the sum of the resource-levels of the four cells that make up the patch drop below 350. This involves turning the food patch black (so it is inaccessible to all agents) and resetting the resource-level to a total of 400. The deplete-num value is increased by one and the deplete-count variable is set to one here as well. The deplete-count is increased by one at every time step until the food patch is made accessible again. It can only be made accessible once deplete-count reaches a value of five or greater and any agent with an energy-level below 50 steps on the food patch.

In Phase 2, the food patch is also depleted when the total resource-level falls below 350. However, in this phase, the food patch is turned yellow (so it is only accessible by the producer) instead of black and the reset-num-for variable is increased by one. The food patch is only made accessible to all agents again the next time the producer feeds.

<u>Updating global variables</u>

The global variables prox-centrality-list, proxim-IDs, and fss-list are updated at the end of each time step. Each of these variables is a list with a length equal to the number of agents in the simulation and each item in the list corresponds to the ID number of each agent. Each agent counts the number of other agents within a radius of two units and enters this number into the appropriate item in the prox-centrality-list. To update proxim-IDs, each agent enters a list of the ID numbers of the agents in proximity to it into the appropriate item in the proxim-IDs list. Finally, to update fss-list, each agent adds the value of its sf-seen variable to the appropriate item in fss-list.

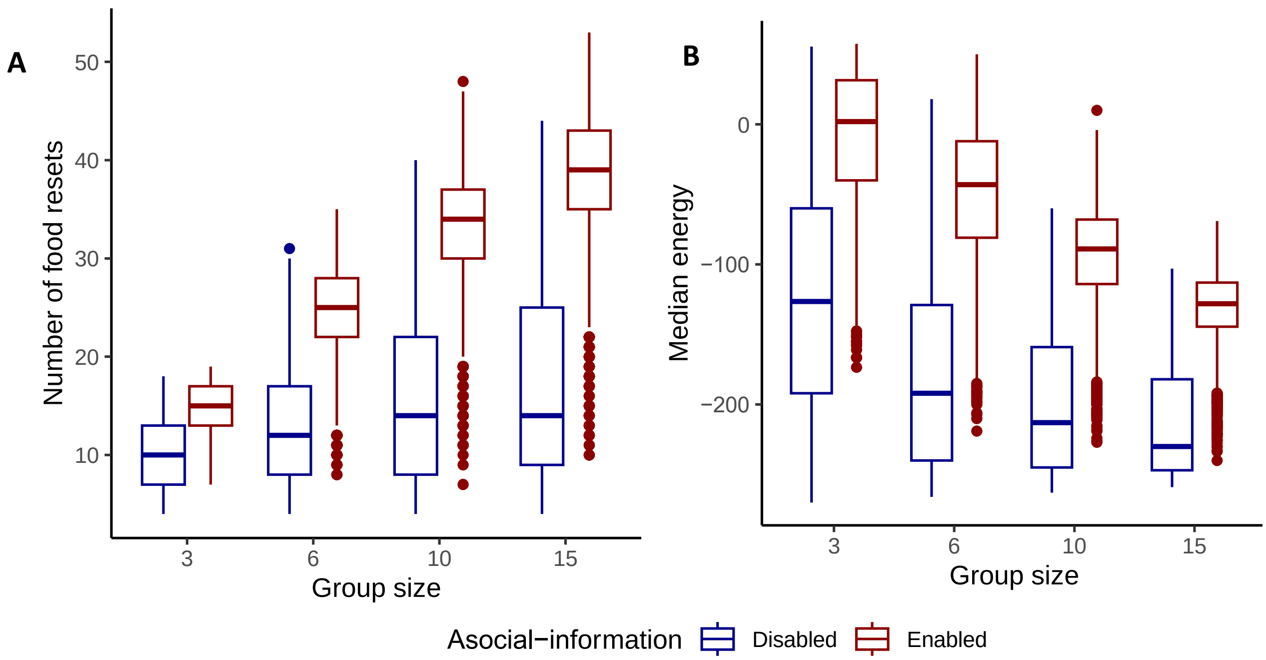

Figure S1. (A) Number of times food patch was reset during the simulation across group sizes. (B) Median scrounger energy levels at the end of simulations across group sizes

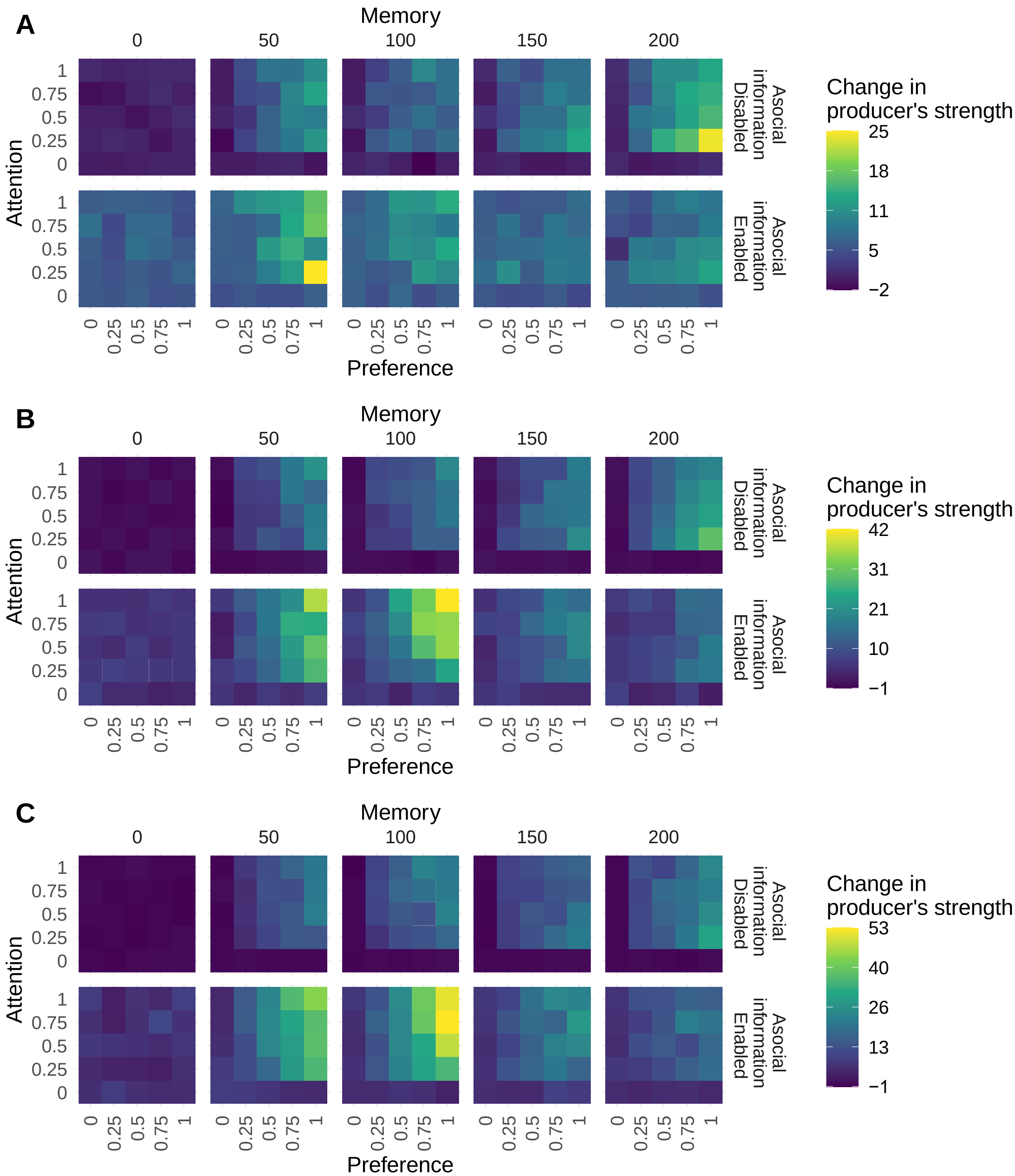

Figure S2. Median change in producer's strength from Phase 1 to Phase 2 across 50 model runs for (A) group size 3, (B) group size 6, and (C) group size 10. This figure corresponds to Fig 2 in the main text.

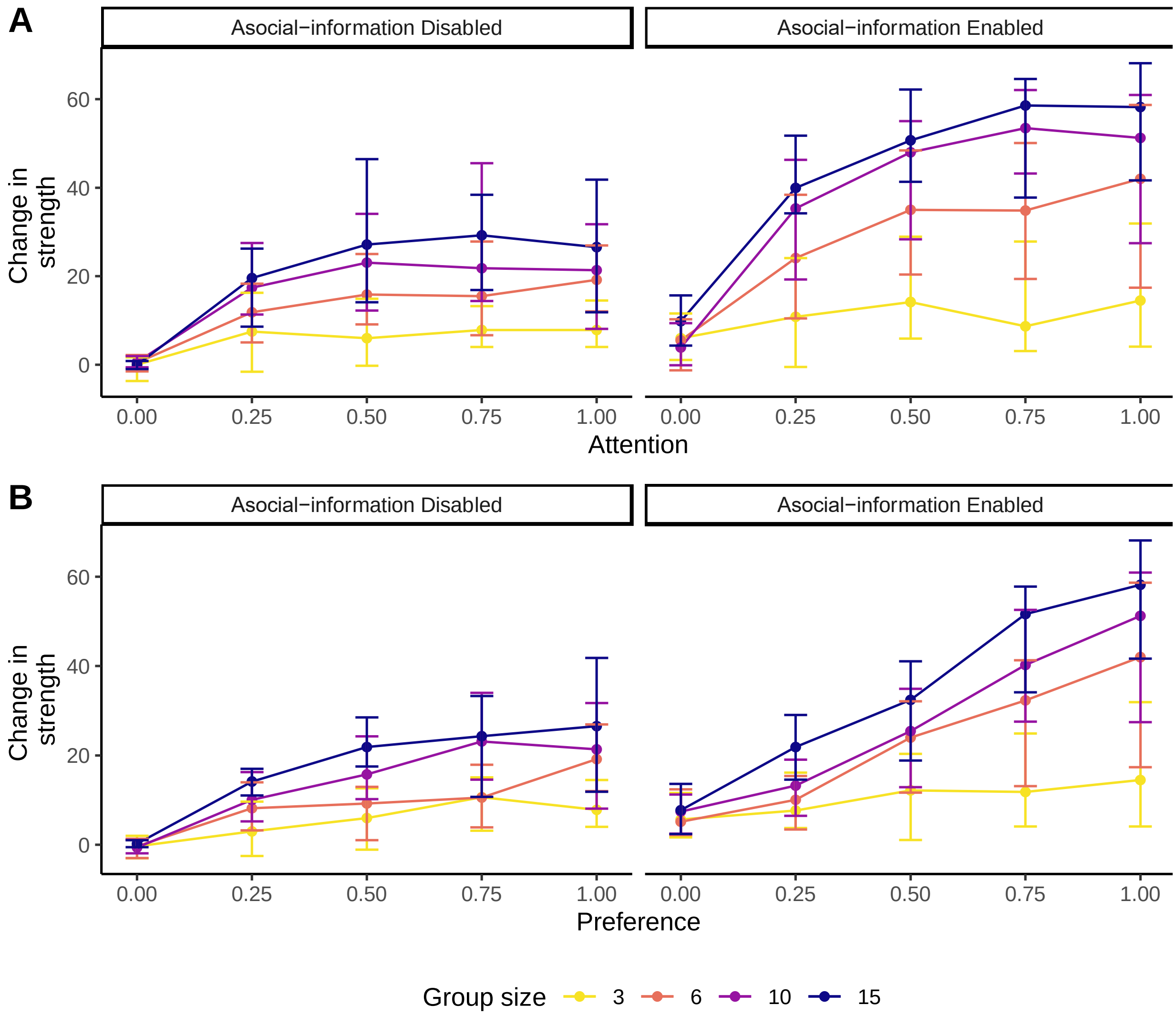

Figure S3. Median and interquartile range of the change in scaled strength between Phase 1 and Phase 2 when varying **(A)** attention while keeping preference at 1 and memory at 100, **(B)** preference while keeping attention at 1 and memory at 100. This figure corresponds to Fig 3 in the main text.

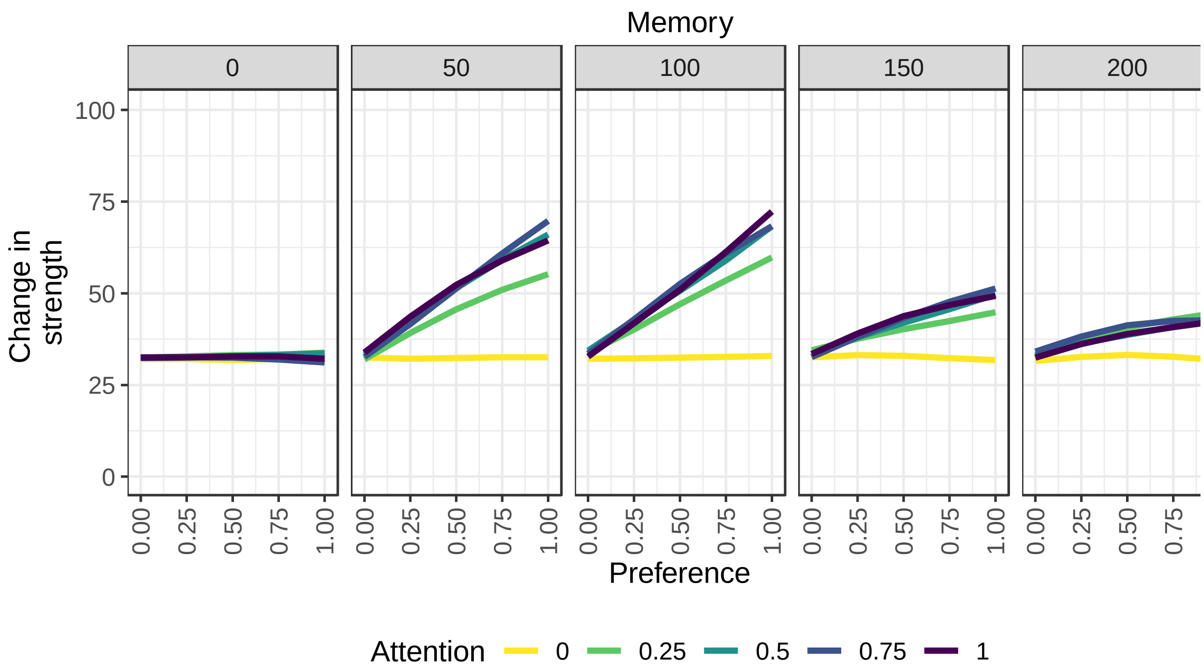

Figure S4. The tensor-product smooth interaction of attention, preference, and memory, showing a synergistic nonlinear effect on the change in scaled strength between Phase 1 and Phase 2. Shaded areas represent the 95% confidence interval. Only data from simulations with a group size of 15 and asocial-information enabled are shown.

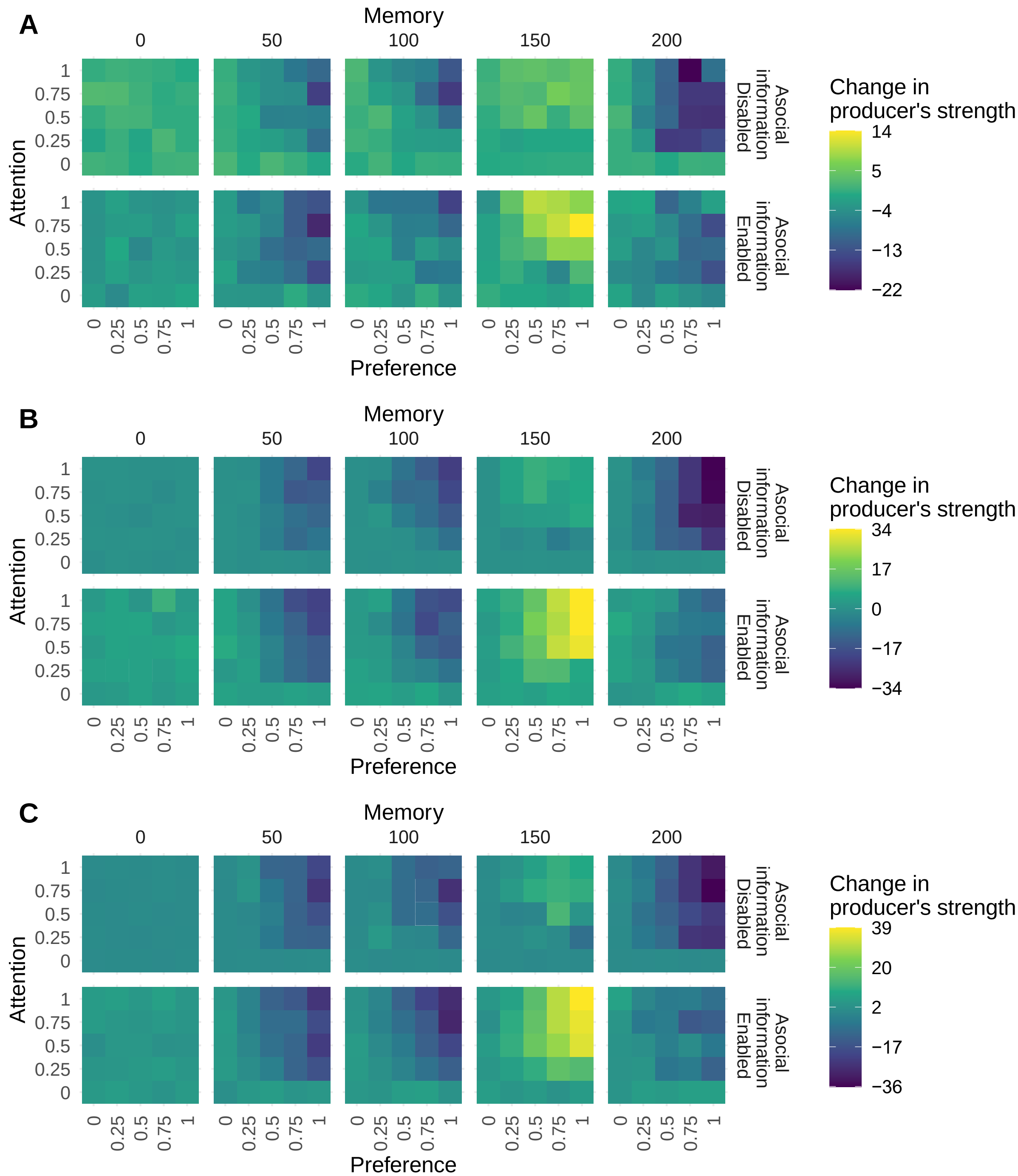

Figure S5. Median change in producer's strength from Phase 2 to Phase 3 across 50 model runs for (A) group size 3, (B) group size 6, and (C) group size 10. This figure corresponds to Fig 4 in the main text.

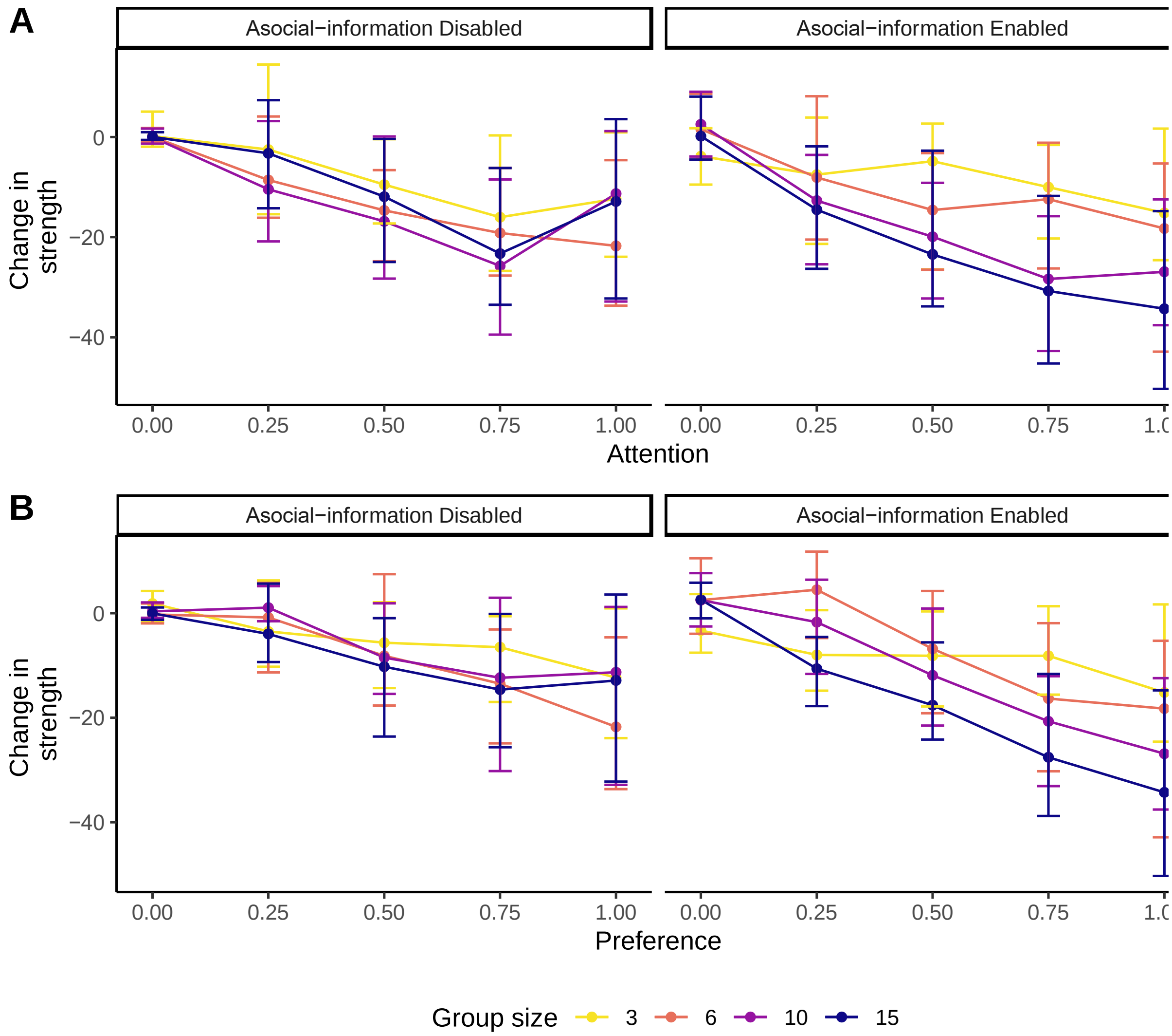

Figure S6. Median and interquartile range of the change in scaled strength between Phase 2 and Phase 3 when varying **(A)** attention while keeping preference at 1 and memory at 100, **(B)** preference while keeping attention at 1 and memory at 100. This figure corresponds to Fig 5 in the main text.

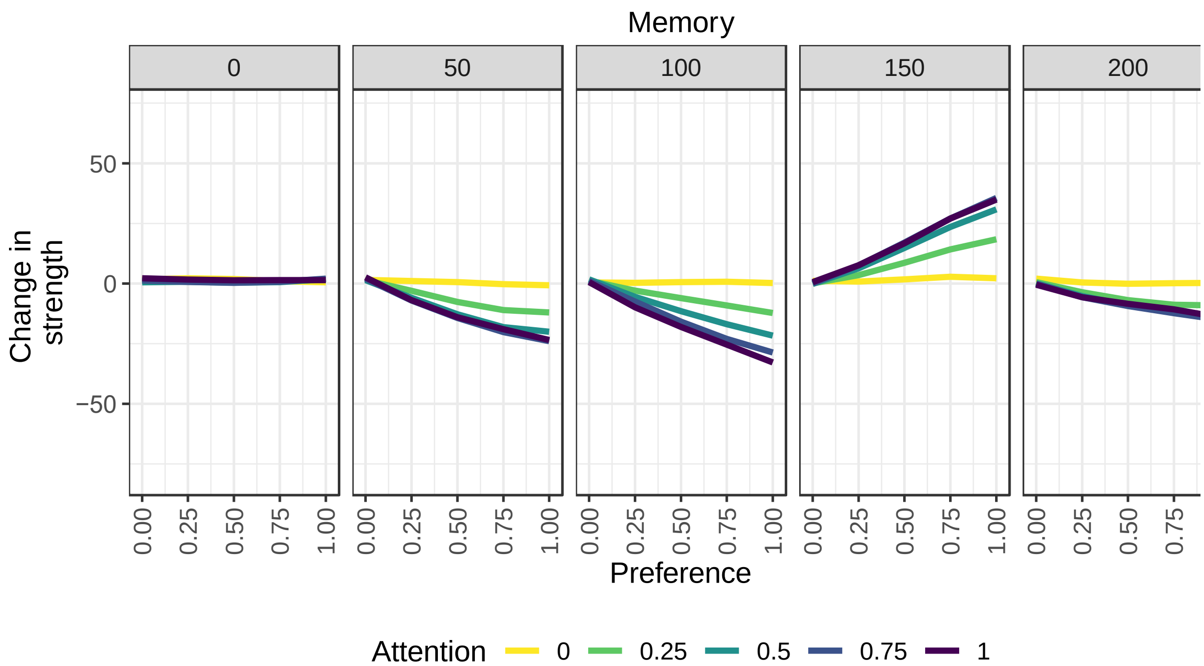

Figure S7. The tensor-product smooth interaction of attention, preference, and memory, showing a synergistic nonlinear effect on the change in scaled strength between Phase 1 and Phase 2. Shaded areas represent the 95% confidence interval. Only data from simulations with a group size of 15 and asocial-information enabled are shown.

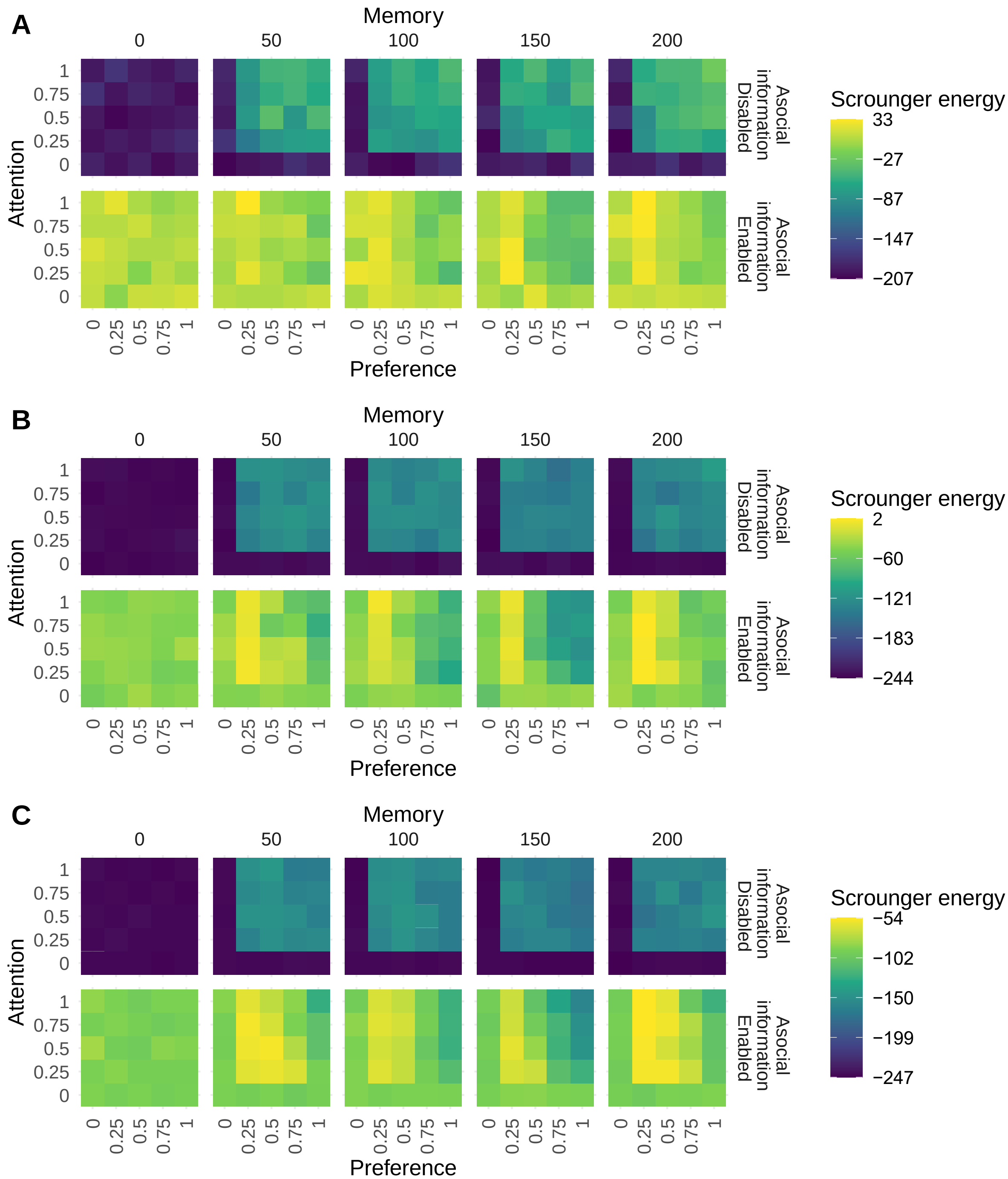

Figure S8. Median scrounger energy across 50 model runs for (A) group size 3, (B) group size 6, and (C) group size 10. This figure corresponds to Fig 6 in the main text.

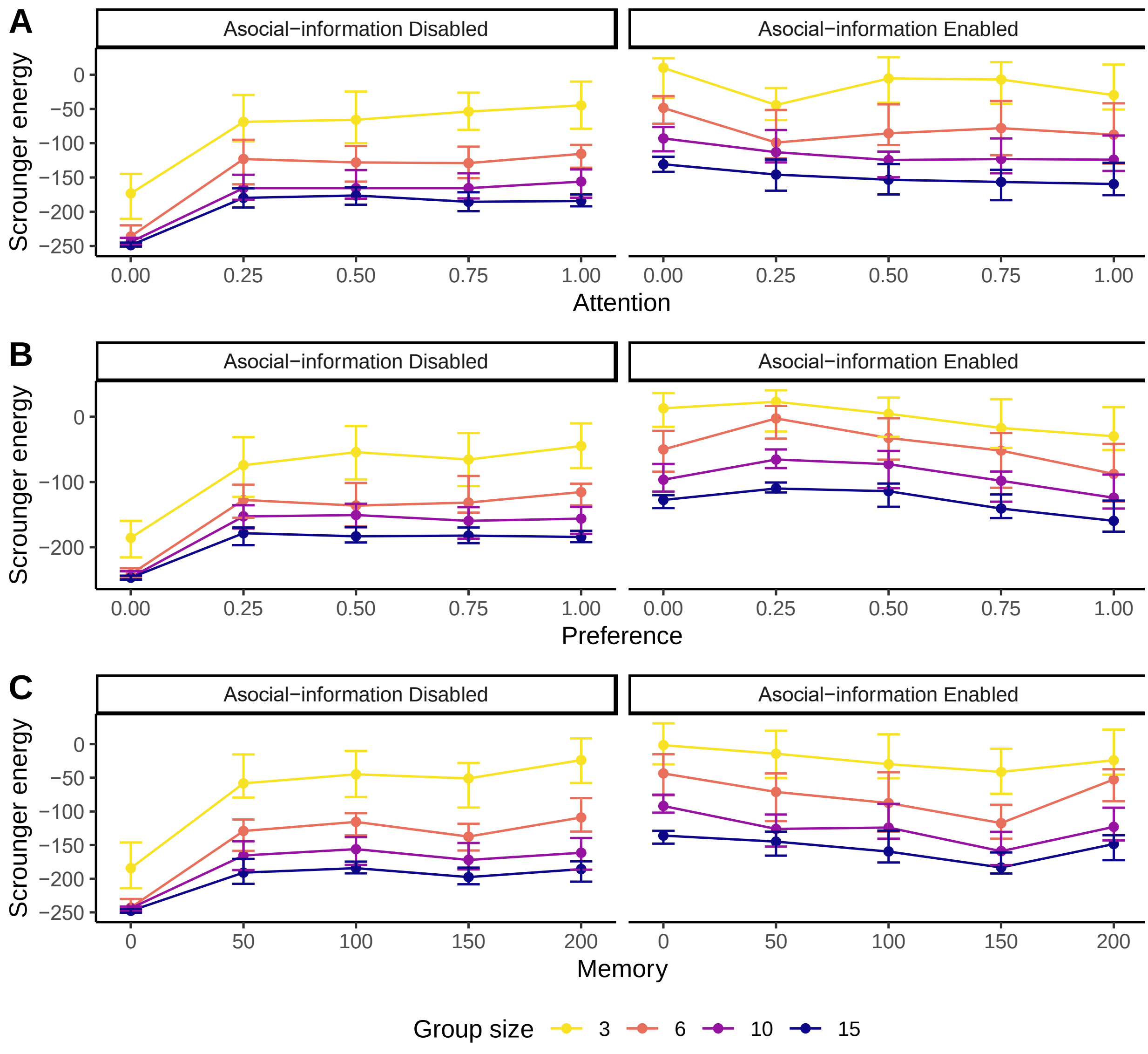

Figure S9. Median and interquartile range of the median energy achieved by scroungers when varying **(A)** attention while keeping preference at 1 and memory at 100, **(B)** preference while keeping attention at 1 and memory at 100, and **(C)** memory while keeping attention and preference at 1. This figure corresponds to Fig 7 in the main text.