

The local enhancement conundrum: In search of the adaptive value of a social learning mechanism



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ABSTRACT

Social learning mechanisms are widely thought to vary in their degree of complexity as well as in their prevalence in the natural world. While learning the properties of a stimulus that generalize to similar stimuli at other locations (stimulus enhancement) *prima facie* appears more useful to an animal than learning about a specific stimulus at a specific location (local enhancement), empirical evidence suggests that the latter is much more widespread in nature. Simulating populations engaged in a producer–scrounger game, we sought to deploy mathematical models to identify the adaptive benefits of reliance on local enhancement and/or stimulus enhancement, and the alternative conditions favoring their evolution. Surprisingly, we found that while stimulus enhancement readily evolves, local enhancement is advantageous only under highly restricted conditions: when generalization of information was made unreliable or when error in social learning was high. Our results generate a conundrum over how seemingly conflicting empirical and theoretical findings can be reconciled. Perhaps the prevalence of local enhancement in nature is due to stimulus enhancement costs independent of the learning task itself (e.g. predation risk), perhaps natural habitats are often characterized by unreliable yet highly rewarding payoffs, or perhaps local enhancement occurs less frequently, and stimulus enhancement more frequently, than widely believed.

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1. Introduction

Social learning and the processes underlying it have long been the center of debates among those studying human and animal behavior and cognition (Zentall and Galef, 1988; Heyes and Galef, 1996; Laland and Galef, 2009; Hoppitt and Laland, 2013). Its great attraction stems from the roles it plays in child development, animal cognition, the evolution of human culture, and from the question of animal culture (Rendell et al., 2011; Hoppitt and Laland, 2013). Key questions associated with these debates include: What are the similarities and differences between human culture and animal social learning and tradition? Do humans deploy more advanced social learning mechanisms compared to other animals? Are these mechanisms the key to understanding the immense success of human culture? And why did some social learning mechanisms evolve in some species, but not in others?

In studying the evolution of social learning, as in studying the evolution of any biological phenomenon, it is useful to identify its levels of complexity. Over the years, the field of social learning has accumulated a long list of underlying processes, ranging from what are thought to be the relatively simple process of local enhancement to what are regarded as more advanced forms of

social learning, such as production imitation (Zentall and Galef, 1988; Whiten and Ham, 1992; Heyes, 1994; Hoppitt and Laland, 2008). While the precise neural underpinnings of social learning processes are not well understood, it would seem highly plausible that some of these mechanisms require greater cognitive capacities than others; indeed, this assumption is widespread in the animal social learning literature. But even among the seemingly simpler mechanisms, empirical studies provide extensive evidence for the existence of some processes, but very little evidence of the existence of others. This is the case for local enhancement and stimulus enhancement, where there are currently far more clear-cut reports of the former than the latter (Hoppitt and Laland, 2008).

Local enhancement occurs “when after, or during, a demonstrator’s presence, or interaction with objects, at a specific location, an observer is more likely to visit or interact with objects in that location” (Hoppitt and Laland, 2008 after Thorpe, 1963). Stimulus enhancement occurs “when observation of a demonstrator (or its products) exposes the observer to a single stimulus at time t_1 , and single stimulus exposure effects a change observed in the observer detected, in any behavior, in time t_2 ” (Heyes, 1994 after Spence, 1937). It has been suggested that local enhancement is a special case of stimulus enhancement (Galef, 1988); however this is highly debatable (Hoppitt and Laland, 2008, 2013) and recent evidence suggest that these are two distinct processes (Webster and Laland, 2012).

Intuitively, stimulus enhancement, or the ability to generalize knowledge of a stimulus at a specific location to similar stimuli

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elsewhere, would appear more beneficial to the learner than acquiring knowledge solely about a specific location alone. However, a recent review of the literature (Hoppitt and Laland, 2008) finds that very few studies incontrovertibly demonstrate stimulus enhancement in animals, whilst in contrast local enhancement appears much more common, and would seem to command far more supportive evidence. Part of the reason for the low occurrence of stimulus enhancement in the literature stems from the difficulty of distinguishing stimulus enhancement from other social learning mechanisms, such as observational conditioning or observational response–reinforcer learning (see Hoppitt and Laland, 2008 for a comprehensive review).

This difficulty in distinguishing between social learning mechanisms, together with the observation that multiple processes may simultaneously be deployed by animals under natural conditions (Hoppitt et al., 2012), raises concerns over the usefulness of current definitions. While, as stated above, it is widely believed that some mechanisms are more cognitively advanced than others, current terms are overlapping, not mutually exclusive, and frequently difficult to distinguish from each other (Hoppitt and Laland, 2008). In light of these difficulties, Hoppitt and Laland (2013) suggest a pragmatic framework for the identification and conceptualization of social learning mechanisms. In this framework, an event of social transmission can be classified by four readily observable criteria: context-specificity, sensitivity to the outcomes of the demonstrator's actions, action-specificity, and novelty of the action or action-sequence. Using these criteria, all current widely discussed social learning processes can be distinguished. The practicality of this method of classification becomes apparent when trying to model the social learning process and break it into its building blocks, as we show here.

In this paper, we set out to explore the ecological conditions that favor stimulus and local enhancement through the use of evolutionary models. To do this, we simulate social learning in the context of a simple social foraging scenario: the producer–scrounger game (Barnard and Sibly, 1981; Giraldeau and Caraco, 2000; Giraldeau and Dubois, 2008). In this game, individuals at any particular point in time can be either producers, who search for resources independently, or scroungers, who follow others in the group and parasitize on their findings. Scrounging may require less time and effort compared to producing, but its success critically depends on the presence of producers in the group; therefore, the two strategies are negatively frequency dependent, resulting in a mixed evolutionarily stable strategy (Barnard and Sibly, 1981).

This game is a useful framework for studying both individual and social learning: when producing, an individual may acquire information about its environment independently while when scrounging, it may acquire information through others (Giraldeau and Caraco, 2000; Arbilly et al., 2011). We assume that an individual's fitness is a positive function of the payoff it has accumulated throughout its lifetime—while producing or scrounging or both. When producing, an individual uses previously learned information to decide which patch to visit, and therefore its producing success relies heavily on its learning strategy: whether it learns individually when producing, whether it learns socially when scrounging, and which learning mechanism (local learning or stimulus learning) is used in either case.

In accordance with Hoppitt and Laland's (2013) framework for identifying mechanisms of social learning, we distinguish between local and stimulus enhancement by the specificity of the context: is the forager learning about the specific location of a patch, or is it learning about a stimulus, such that it can generalize the knowledge it acquires to similar stimuli at other locations? Strictly, this criterion alone is insufficient to exclude other social learning mechanisms. Nonetheless we believe that this distinction is a practical first step in exploring the evolution of these social learning

mechanisms. Hence what we characterize as conditions that favor stimulus enhancement may more accurately be described as conditions that favor stimulus enhancement or other social learning mechanisms that are stimulus-specific (e.g. observational conditioning). We address this issue further in the discussion.

2. The model

2.1. The population

We simulated a population of $n = 100$ social foragers. For mathematical convenience we assume haploid genetics. We specify that the behavior and learning abilities of each individual are influenced by three genes: (1) F , a social foraging gene, which determines its carrier's probability of using the producer, and (complementarily) the scrounger strategy (hence $1 - F$ is the probability of using the scrounger strategy). We assume 11 possible alleles in this gene (F_0, F_1, \dots, F_{10}), ranging from pure scrounging (F_0), through mixed strategies of producing and scrounging (F_1 – F_9 where F_1 codes for 10% probability of producing and 90% probability of scrounging, F_2 for 20% producing and 80% scrounging, etc.), to pure producing (F_{10}). (2) I , an individual learning gene, which determines the learning mechanism used when a forager plays the producer strategy. This gene has three possible alleles: non-learning (I_0), individual local learning (I_1), or individual stimulus learning (I_2). (3) S , a social learning gene, which determines the learning mechanism deployed when a forager plays the scrounger strategy. This gene also has three possible alleles: non-learning (S_0), learning by local enhancement (S_1) or learning by stimulus enhancement (S_2).

In all simulations, in the first generation the population carried each F gene allele with equal probability, but the I_0 allele and the S_0 allele were fixed (i.e. agents were complete non-learners). Learning alleles I_1 , I_2 , S_1 and S_2 were introduced in subsequent generations via random mutation.

A generation was composed of T time steps; at each step agents were allotted a social foraging strategy (probabilistically, according to their F genotype). After T steps, foragers were ranked according to the payoff they had accumulated throughout their lives, and the top 50% gave rise to the next generation (truncation selection). We assumed that each surviving agent produced two genetically identical offspring. These offspring were subjected to random mutation occurring in all three genes at a rate $\mu = 1/n$ (i.e. 0.01) per generation. Once the new generation was produced, the parental generation died, maintaining the population at a constant size.

2.2. The environment

The environment was composed of $H = 100$ food patches, each belonging to one of three types: E_1 , E_2 and E_3 , occurring at equal probability (0.33). The locations of patches belonging to each type were shuffled for each new generation, but remained constant across a generation's lifetime. Patch types differed in the value of the food items they provided, the probability of obtaining these items, and their overall expected payoff. To simulate a non-trivial, yet natural, learning task, we assumed a negative relationship between the value of the food item and the probability to obtain it. That is, the most valuable food items were assumed to be the least likely to be found, but on average the patches that contained valuable food items were the most profitable. Recurring failures to find food in these most profitable patches serve a number of purposes: they necessitate repeated sampling for proper evaluation of the patches, and they provide an inherent disadvantage to the pure producing strategy (see Arbilly et al., 2010 for analysis); this, consequently, gives social learning an advantage over individual learning

(Arbilly et al., 2011). We assume that E_1 contained food items with a nutritional value of 0.25 which could be found with probability 1 (expected value 0.25), and E_2 contained food items of value of 1 with probability 0.5 (expected value 0.5). E_3 , the highest-paying patch type, had the lowest food-obtaining probability. The probability of obtaining food items in E_3 was always 0.25, but we tested three possible expected values: 1, 2 and 3 (food items value 4, 8 and 12, respectively).

We assume that the three patch types can be distinguished from each other using some cue (e.g. visual or olfactory). Foragers could also distinguish between specific patches by their location. In order to affect the efficiency of learning via stimulus enhancement, the reliability of the cue as a predictor of patch type was manipulated using the parameter c . When creating a new environment for any new generation, c was the probability that the payoff found in a specific patch that was associated with a specific cue, will also be found in any other patch associated with the same cue. At its highest value $c = 1$, correlation of cue and payoff was perfect and patches of type E_1 were associated with one cue, patches of type E_2 were associated with a second cue, and patches of type E_3 were associated with a third cue. At its lowest value $c = 0.33$, there was no correlation between cue and payoff: the three cues were randomly assigned to patches regardless of patch type.

To examine the possible effects of environmental spatial structure on the question at hand, we considered both spatially structured and a non-spatial environments. In both cases, foragers chose patches to produce in based on their memory, and when scrounging, joined successful producers randomly. In the non-spatial case, we assumed that movement between patches was simple and not costly: foragers had no constraints in choosing patches when producing or in choosing producers to join when scrounging. In the spatially structured environment foragers were living on a 10×10 patch grid and could only move between adjacent patches. In most cases this gave a forager nine possible patches to move between (its current patch and the square of eight patches surrounding it), but its options were reduced to either six patches if it was on one of the grid's edges, or four patches if standing in a corner. This limited options both when choosing a patch as a producer, and when joining a producer when scrounging.

2.3. The producer–scrounger game

Each time step started with all foragers drawing either a producer or a scrounger strategy for that step, with a probability specified by their F genotypes. Foragers who drew the producer strategy then chose a patch in which to search for food. In a generation's first step, this choice was random, as foragers had no information about the patches. In the spatial simulations, choice in the first step positioned all producers on the grid for the first time. From the second step onward, producers' choice (if they were learners) was based on previous experience, according to the decision rule specified below. In non-spatial simulations, producers could choose any patch in the environment, while in spatial simulations they could only choose between their current patch and the patches immediately adjacent to it. There was no limit to the number of producers who could forage in a single patch. After choosing a patch, producers received a payoff, or did not, based on the food-obtaining probability in their chosen patch. Subsequently, foragers who drew the scrounger strategy attempted to join the producers who found food. In the first step of all simulations, and in all steps of non-spatial simulations, assignment to a producer was completely random and independent: all scroungers “chose” simultaneously who to join from a pool of successful producers. In spatial simulations, from the second step onward, scroungers could only try to join producers in their current patch or the patches immediately surrounding it, and if there was no successful producer in

their neighborhood they moved to an adjacent patch, chosen at random, but received no payoff. In both types of simulations, we assume that each producer could only be joined by one scrounger, and in the case of multiple scroungers attempting to join a single producer, only one of them (picked at random) received a payoff, with the others moving to the producer's patch receiving nothing. A joined producer kept a finder's share proportion of the food item it found, and the scrounger joining it received the remainder. In most simulations, the finder's share was half the payoff.

2.4. Learning abilities

We assumed that all foragers had a “memory map” of all patches in the environment, all initially set to the same value (the mean of all patches' expected payoffs). Foragers carrying learning ability alleles updated the payoff they received upon visiting a patch as producers, or the payoff they had observed the producer receive as scroungers, in their memory. Foragers carrying local learning alleles (I_1 for individual learning and S_1 for social learning) updated the received payoff in their memory of the specific patch visited. Foragers carrying stimulus learning alleles (I_2 for individual learning and S_2 for social learning) updated the received payoff in their memory of the type of patch visited (technically, this meant updating the payoff in the forager's memory of all patches of this type).

Payoff Y_t acquired in patch x at step t updates the memory cell M_x using a linear operator rule (McNamara and Houston, 1987; March, 1996; Beauchamp, 2000; Eliassen et al., 2009) of the form: $M_{x,t} = \alpha M_{x,t-1} + Y_t(1 - \alpha)$, where α is a recency factor representing the weight of previous payoffs in memory (set to 0.5 in all simulations). This learning rule is used both when producing and when scrounging: when producing the updated payoff Y_t is the initial payoff found by the producer before the arrival of a scrounger; when scrounging, Y_t is the divided payoff observed by the scrounger (which, since the payoff is divided equally by the producer and the scrounger, is identical to the payoff the scrounger receives). Producing and scrounging experiences in a specific patch are updated in the same memory cell, and the forager does not distinguish between individually and socially acquired information. It should be noted that memory is updated for the visited patch alone, and memory for all other patches remains unchanged.

To account for the possibility that scrounging interferes with learning (Giraldeau and Lefebvre, 1987; Fragasz and Visalberghi, 1990; Beauchamp and Kacelnik, 1991; Nicol and Pope, 1994), due to for example, some attention being directed to the social interaction or because the patch's cue is not experienced as intensely when following others, we assume some social learning error probability θ . This is the probability of attributing the payoff observed while scrounging to a patch other than the one visited. Error was in accordance with the scrounger's social learning mechanism. In the case of local enhancement, in spatial simulations, the payoff was erroneously attributed to one of the adjacent patches; in non-spatial simulations, the payoff could be erroneously attributed to any patch in the environment. In the case of stimulus enhancement, both in spatial and non-spatial simulations, the payoff was erroneously attributed to another patch type.

2.5. Decision rule

When playing producer, a forager chooses a patch in which to search for food based on prior knowledge of all relevant patches. The probability p of choosing patch x at time $t + 1$ is calculated using an exponential ratio decision rule (following Ben-Akiva and Lerman, 1985; Bereby-Meyer and Erev, 1998; Bussemeyer and Myung, 1992; Camerer and Ho, 1999), weighting the forager's

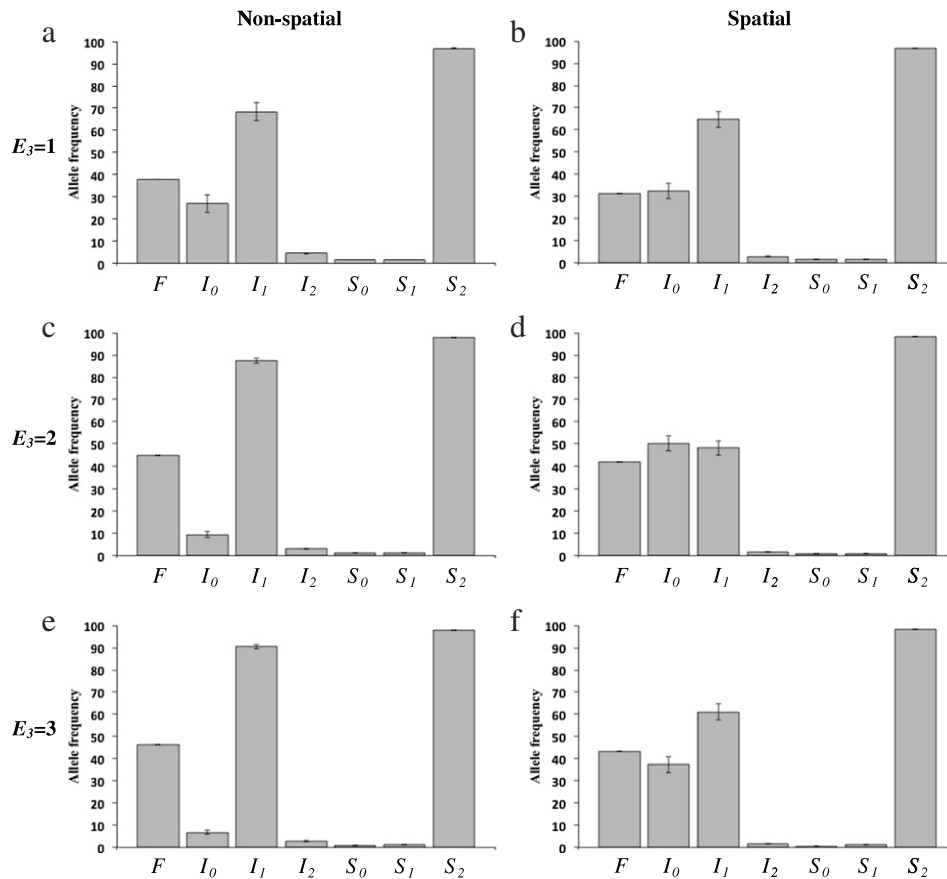


Fig. 1. Mean scrounging frequency and mean frequencies of learning alleles when cues are perfectly correlated with payoffs ($c = 1$) and learning is without error ($\theta = 0$). Left column shows means for non-spatial simulations, right column shows means for spatial simulations. Means and standard errors are calculated for generations 1001–2000 over 10 repeats of each simulation. Population size $n = 100$, patch number $H = 100$, number of time steps $T = 50$.

information M of patch x at time t against information of all relevant patches 1 through k :

$$p_{x,t+1} = \frac{e^{M_{x,t}}}{\sum_{i=1}^k e^{M_{i,t}}}.$$

In non-spatial simulations the summation $1 \dots k$ is over all 100 patches in the environment. In spatial simulations, the summation is only over patches in the forager's immediate surroundings (including the current patch, which it visited at step t). We use this decision rule because it provides greater choice flexibility and allows agents some probability of revisiting patches that they have previously failed to obtain payoff in. It should be noted that learning mechanisms are irrelevant in the decision-making process: agents choose to produce in a specific patch and not in a specific patch type.

3. Results

3.1. Flawless social learning in environments with reliable cues

When cues were reliable predictors of payoff ($c = 1$) and social learning was without error ($\theta = 0$), populations in both spatial and non-spatial simulations engaged in a stable producer–scrounger game, and scrounging frequency was correlated with the expected payoff of the highest-paying patch, E_3 : the higher the expected payoff, the higher the scrounging frequency (Fig. 1). The most frequent allele of the F gene was the mixed-strategy allele corresponding to the population's mean scrounging frequency (e.g. if the mean producing frequency was ~ 0.6 , the prevalent allele

was F_7 coding for 0.6 producing probability). Producing frequency in spatial simulations was slightly higher than in non-spatial simulations as was to be expected, as scroungers had far fewer joining options when they could only join successful producers in their immediate surroundings (Fig. 1).

All populations (spatial and non-spatial) evolved stimulus enhancement (allele S_2) as their social learning mechanism (Fig. 1). In non-spatial simulations, foragers evolved local learning (allele I_1) for their individual learning mechanism (Fig. 1, left column), while in spatial populations we observed a mixed equilibrium of local learning and non-learning (alleles I_1 and I_0 ; Fig. 1, right column). The difference once again stems from the freedom of movement in non-spatial simulations. In an environment where the most variable patches are also the best patches on average, it is better to learn socially, while scrounging: this means learning only from success and circumventing risk aversion, thus visiting the best patches when producing despite repeated failures (Arbilly et al., 2011). Foragers in non-spatial simulations, if they remembered that they failed in a patch that happens to be of the best type, would still have plenty of other patches of this type that they might visit, by chance; in one of these visits they are likely to receive the large payoff this patch type offers, and this will significantly increase their probability of revisiting this specific patch. This explains the advantage local learning (I_1) has over non-learning (I_0) in non-spatial simulations. In spatial simulations, foragers are restricted to moving between adjacent patches and therefore have less patches to choose from at any given step, which increases the advantage of not learning individually at all (i.e. allele I_0) and acquiring information only while scrounging (since while scrounging one learns only from successful producers).

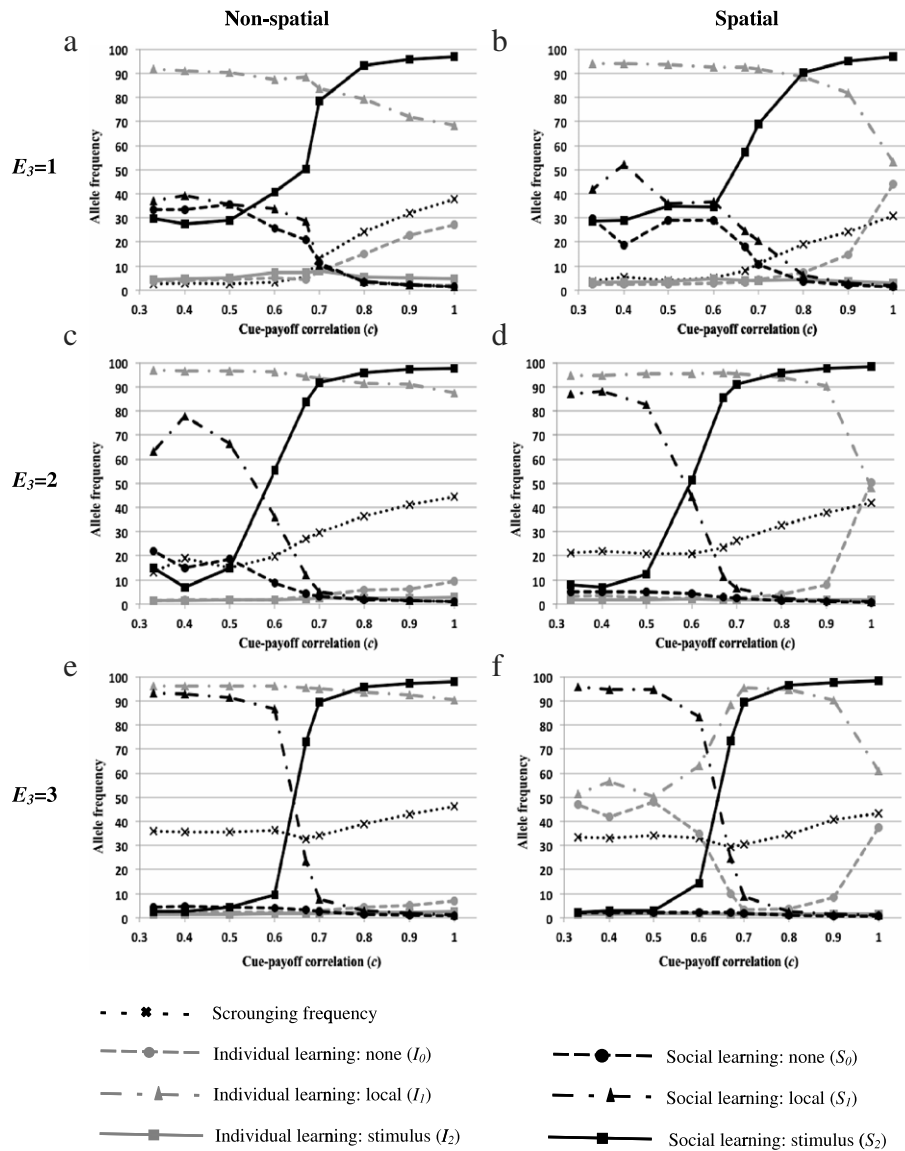


Fig. 2. Mean scrounging frequency and mean frequencies of learning alleles as functions of cue-payoff correlation c , in three environments differing in the expected payoff of the highest-paying patch type, E_3 . Left column shows means for non-spatial simulations, right column shows means for spatial simulations. Means are calculated for generations 1001–2000 over 10 repeats of each simulation. Population size $n = 100$, patch number $H = 100$, number of time steps $T = 50$.

Varying the frequency of each patch type yielded similar results. Decreasing the number of time steps, or introducing within-generation environmental change both led to a decrease in scrounging and social learning, as predicted by previous studies (Aoki et al., 2005). These populations still evolved stimulus enhancement as their social learning mechanism.

3.2. Environments with unreliable cues

To challenge the effectiveness of stimulus enhancement, we next tested the effect of reducing cue reliability c (while maintaining social learning without error $\theta = 0$). As we decreased c , all populations decreased in scrounging frequency. The decrease was much more pronounced for $E_3 = 1$, where scrounging became extinct at $c \sim 0.6$ in both spatial (Fig. 2(a)) and non-spatial simulations (Fig. 2(b)). These results are in line with previous studies showing that heterogeneous environments promote individual learning (Aoki and Nakahashi, 2008).

The social learning mechanism evolving in all populations remained stimulus enhancement until cues were reliable less than

two out of three times ($c < 0.67$), at which point populations where scrounging survived (at $E_3 = 2$ and $E_3 = 3$) evolved local enhancement (allele S_1 ; Fig. 2(c)–(f)). For $E_3 = 1$, the three social learning alleles appeared at roughly similar frequencies, suggesting genetic drift, as scrounging reappeared via random mutation and quickly became extinct again (Fig. 2(a)–(b)).

In non-spatial simulations, there was no change in individual learning mechanism, and local learning (I_1) maintained its high frequency as we varied cue-payoff correlation c (Fig. 2, left column). In spatial simulations, as c decreased and with it the frequency of scrounging and social learning, local learning (I_1) gained an advantage over non-learning (I_0) and became the prevalent individual learning mechanism (Fig. 2(b), (d), (f)). The change is sharp: when patches' payoff can be reliably predicted by cue ($c = 1$), local learning (I_1) is as good as non-learning (I_0), but as soon as the reliability of cues is less than perfect ($c = 0.9$) local learning (I_1) is much better than non-learning (I_0). Since the reliability of cues c does not affect the quality of information acquired through local learning (but only information acquired through stimulus learning), this change suggests that individual local learning (I_1) improves the overall quality of information, “fixing” the problems

caused by social stimulus learning (S_2) in an unpredictable environment. So it appears that the decrease in environmental predictability does have an effect, but interestingly, stimulus enhancement together with the quality compensation provided by individual learning appears to be more adaptive than evolving local enhancement as a social learning mechanism under these conditions.

When $E_3 = 3$, non-learning regains an advantage as c becomes small, and a mixed equilibrium of I_1 and I_0 emerges once again (Fig. 2(f)). This mixed equilibrium emerges simultaneously with the increase in social learning via local enhancement (S_1): social local enhancement provides reliable information regardless of cue reliability; therefore, there is no longer a need to correct for the poor quality of social information; once there is no longer such a need, individual non-learning and individual local learning provide roughly the same advantage. That this pattern arises here but not when $E_2 = 2$ seems to be related to the high stakes involved: the higher the risky payoff, the better it is to not remember failures.

It should be noted that scrounging can be maintained in environments where $E_3 = 1$, allowing local enhancement to evolve when c is small, by manipulating various parameters. One possibility is decreasing the finder's share (kept at 0.5 in all simulations) thus permitting scroungers to gain more than the producers they join (not shown). Yet another is to reduce the number of patches in the environment (in both spatial and non-spatial simulations), therefore increasing the probability of revisiting a patch (Fig. 3). When the number of patches is very small, populations noticeably do not learn individually at all (I_0), in line with previous results (Arbilly et al., 2011).

3.3. Impaired social learning

To test whether reduced quality of social information may give an advantage to local enhancement over stimulus enhancement, we increased the probability of error in social learning, θ (while cues remained perfect predictors of payoff, $c = 1$). As θ increased, scrounging decreased in frequency; for $E_3 = 1$, it became extinct at $\theta > 0.5$ in both spatial and non-spatial simulations (Fig. 4(a)–(b)). In these populations, the three social learning mechanisms once again show a genetic drift pattern, due to random mutations reintroducing scrounging into the population and quickly disappearing.

In populations where scrounging survived (environments where $E_3 = 2$ or $E_3 = 3$), stimulus enhancement (S_2) was replaced by local enhancement (S_1) as social learning error initially increased in rate, but as the rate became high, local enhancement and non-learning (S_0) were observed at similar frequencies (Fig. 4(c)–(f)). In all environments, as social learning error rate θ increased and social information became unreliable, foragers evolved stimulus learning (I_2) as their individual learning mechanism (Fig. 4).

4. Discussion

Several recent reviews of animal social learning in diverse taxa concluded that local enhancement is widespread in nature (Hoppitt and Laland, 2008; Laland and Galef, 2009; Laland et al., 2011; Rendell et al., 2011). However, while social learning studies in animal behavior point towards high prevalence of local enhancement and low occurrence of stimulus enhancement, our results suggest that in fact local enhancement may only have an advantage under very limited, and sometimes extreme environmental conditions. In an environment where high payoffs are associated with high risk of failure, shown previously to be highly supportive of social learning (Arbilly et al., 2011), scrounging, and with it social learning, becomes extinct as soon as stimulus enhancement is no longer useful

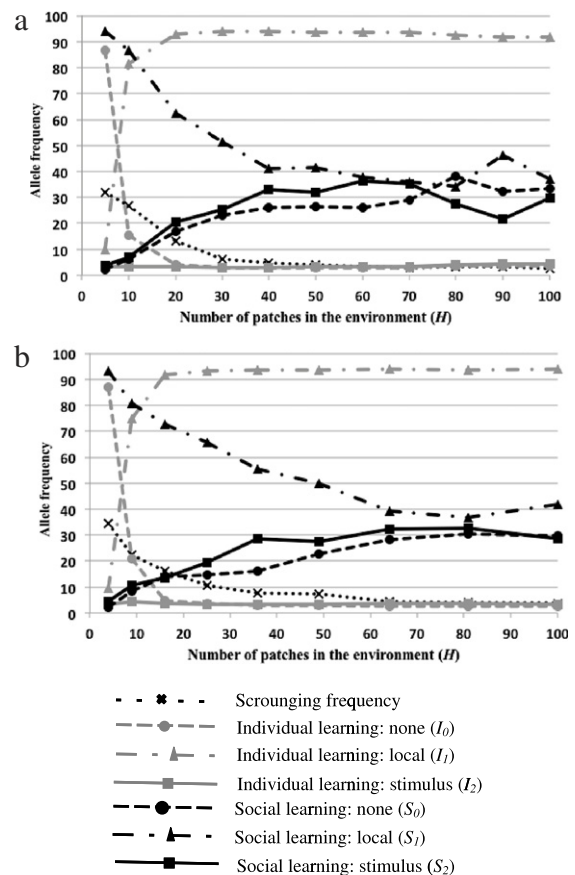


Fig. 3. Mean scrounging frequency and mean frequencies of learning alleles as functions of the number of patches in the environment H . Means are calculated for generations 1001–2000 in 10 repeats of each simulation. Population size $n = 100$, number of time steps $T = 50$, cue–payoff correlation $c = 0.33$. (a) Non-spatial simulations. (b) Spatial simulations.

(cue–payoff correlation c is low), rather than switching the population to local enhancement. For scrounging and local enhancement to coevolve under low cue–payoff correlation, the payoff in the highest-paying patch type must be several times higher than that of any other patch types. This same requirement holds when cue-generalization, and therefore stimulus enhancement, is useful ($c = 1$), but social information is not reliable (large θ), and even then, only in a limited range of social learning error rates. Why does scrounging, and with it social learning, so readily become extinct when it seems that the model conditions should support the advantage of social learning by local enhancement?

The answer lies in the relationship between the number of patches in the environment, and the time provided to explore it. If the number of patches H is large compared to the time available to a forager to study the environment (the number of time steps, T), a situation where cues do not predict payoffs leaves foragers with little knowledge about most patches, even if they update their knowledge at every step, at least until a very late stage in their lives. Therefore even when scrounging in the best patch, the probability of choosing to visit this specific patch when producing, compared to the probability of visiting all (mostly unfamiliar) other patches, is quite small. In spatial simulations, movement is limited to adjacent patches so the probability of revisiting this patch is higher, but it is still small compared to the probability of visiting all adjacent patches, and only two time steps are needed for this patch to no longer be adjacent. This situation results, in both spatial and non-spatial simulations, in reduced success in producing, which subsequently diminishes the payoff scroungers can obtain from producers. This leads to the extinction of scrounging. It

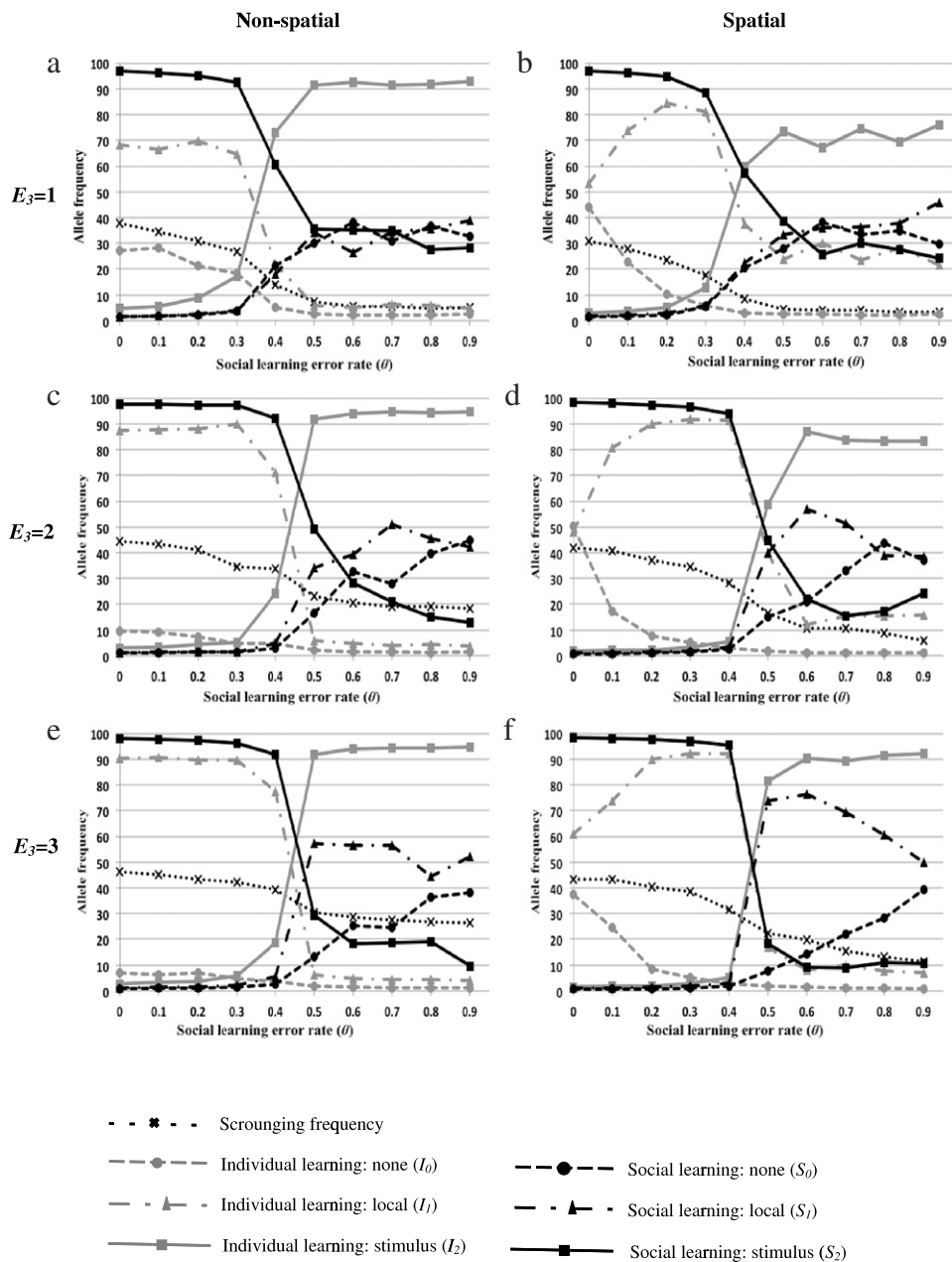


Fig. 4. Mean scrounging frequency and mean frequencies of learning alleles as functions of social learning error rate θ , in three environments differing in the expected payoff of the highest-paying patch type E_3 . Left column shows means for non-spatial simulations, right column shows means for spatial simulations. Means are calculated for generations 1001–2000 in 10 repeats of each simulation. Population size $n = 100$, patch number $H = 100$, number of time steps $T = 50$.

is easy then to understand why a significantly higher payoff in the best patch supports scrounging as well as social learning by local enhancement: the payoff must be outstanding in order to generate a high probability of revisiting the patch, and have the synergistic effect of increasing the success of producing, supporting scrounging and making socially acquired information highly valuable. This explanation is supported by the evolution of local enhancement in environments composed of a small number of patches (Fig. 3).

There are a number of possible interpretations for the discrepancy between our results and current findings on the occurrence of local enhancement and stimulus enhancement in nature. One possibility is that the limited conditions we found to support local enhancement are in fact widespread in nature, or are at least widespread in experimental contexts in which animal social learning is studied. If this is correct, it leads to the prediction that either social learning is highly erroneous, or that environmental contexts

that support local enhancement should have the following properties: patches belonging to the same type do not share a common cue that allows them to be distinguished from other patch types, and they either (1) are few in number relative to the time foragers have to explore the environment, so that the probability of revisiting a patch is high, or (2) the highest paying patch type is better by far than other patch types, giving scrounging an advantage that allows it to evolve alongside producing (or any other conceivable setup that would make scrounging more beneficial).

Another possible explanation for the discrepancy is that there are factors not considered in the model that play a role in the adaptability of local enhancement. For example, it is possible that the ability to generalize between stimuli is more costly than the ability to learn about a location. A potentially relevant issue not considered in our model is predation risk. To make use of stimulus enhancement, animals may be forced to explore new patches

simply because they are similar to a familiar patch which gave a high payoff. But uncharted territory may be dangerous—the cue may reliably predict the payoff, but not potential predators. Where predation risk is high, animals may be better off visiting only familiar patches, a behavior which would be taken as indicative of local enhancement.

A third possibility is that our modeling approach is responsible for the gap between our results and the experimental literature. Conceivably local enhancement is more prevalent in contexts that are not well characterized as producer–scrounger games, or where social learning does not occur as a result of scrounging. We used the producer–scrounger game as the backbone of this model, as it describes a basic and rather ubiquitous form of social interaction. The producer–scrounger game has been documented across species from insects to humans, and seems to capture well the relationship between individual and social learning. However, acquiring information socially does not necessarily involve a payoff (e.g. Rendell et al., 2010), since many animals are capable of learning through observation alone. Indeed, rather than learning through scrounging, there is evidence that scrounging can hinder social learning in some species (pigeons, Giraldeau and Lefebvre, 1987; capuchin monkeys, Frigaszy and Visalberghi, 1990; zebra finches, Beauchamp and Kacelnik, 1991; chickens, Nicol and Pope, 1994), but there is also evidence that it may facilitate learning (titmice, Sherry and Galef, 1984; black rats, Aisner and Terkel, 1992; Norway rats, Laland and Plotkin, 1991; common ravens, Fritz and Kotrschal, 1999; common marmosets, Caldwell and Whiten, 2003; meerkats, Thornton and Malapert, 2009). Given the widespread nature of the producer–scrounger game, it seems a likely framework for the spread of social information. Conceivably, stimulus enhancement might be found more readily in those species showing facilitatory effects of scrounging on social learning.

Finally, a fourth possibility, which seems quite plausible, is that stimulus enhancement is rarely identified in social learning studies because it is hard to tease apart from other social learning mechanisms (Hoppitt and Laland, 2008). On one hand, this may mean that experiments testing for the use of this mechanism must be carefully planned in order to rule out other possibilities. On the other hand, perhaps the strong evolutionary advantage stimulus enhancement maintains across various conditions in our model lends yet more support to the idea that social learning mechanisms need to be assessed and defined using a more practical approach, identifying the elements that are important for the understanding of the process.

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