Can You Trust Who You See? The Evolution of Socially Cued Anticipatory Plasticity

Elizabeth C. Lange,[1,*] Joseph Travis,[1] Kimberly A. Hughes,[1] and Leithen K. M'Gonigle[1,2]

1. Department of Biological Science, Florida State University, Tallahassee, Florida 32306;   2. Department of Biological Sciences, Simon Fraser University, Burnaby, British Columbia V5A 1S6, Canada

ABSTRACT: The social environment can affect development and fitness. However, we do not know how selection acts on individuals that cue developmental pathways using features of the social environment. Socially cued anticipatory plasticity (SCAP) is a hypothetical strategy whereby juveniles use social cues to alter development to match their adult phenotype to the social environment that they expect to encounter. While intuitively appealing, the evolution of such plasticity is a puzzle, because the cue changes when individuals use it. Can socially cued plasticity evolve when such a feedback occurs? We use individual-based simulations to model evolution of SCAP in an environment that fluctuates between favoring each of two discrete phenotypes. We found that socially cued plasticity evolved, but only when strong selection acted on survival rather than on fecundity differences between adult phenotypes. In this case, the social cue reliably predicted which phenotype would be favored on maturation. Surprisingly, costs to plasticity increased the range of conditions under which it was adaptive. In the absence of costs, evolution led to a state where SCAP individuals could not effectively respond to environmental changes. Costs to plasticity lowered the proportion of the population that used SCAP, which in turn increased the reliability of the social cue and allowed individuals that used socially cued plasticity to switch between the favored phenotypes more consistently. Our results suggest that the evolution of adaptive plasticity in response to social cues may represent a larger class of problems in which evolution is hard to predict because of feedbacks among critical processes.

Keywords: social environment, phenotypic plasticity, alternative phenotypes, fluctuating environment, socially cued anticipatory plasticity.

Introduction

Phenotypic plasticity, the ability of an individual to alter its phenotype in response to an environmental cue, is thought to be widespread (Scheiner 1993; Pigliucci 2001, 2005; West-

* Corresponding author; email: elange@bio.fsu.edu.
  ORCIDs: Lange, https://orcid.org/0000-0001-6834-9207; Travis, https://orcid.org/0000-0002-2419-5020.

Eberhard 2003). How much of this plasticity is adaptive remains controversial (Palacio-López et al. 2015). Plasticity can be reversible, allowing an individual to modify its phenotype in response to environmental changes throughout its life, or irreversible, with a phenotype becoming fixed during development. Existing theoretical work on the topic has largely focused on identifying when extrinsic environmental conditions (often abiotic) favor phenotypically plastic, but developmentally irreversible, strategies over nonplastic ones (Levins 1963; Via and Lande 1985; Lively 1986; Moran 1992; Berrigan and Scheiner 2004; Scheiner and Holt 2012; Botero et al. 2015; Chevin and Lande 2015; Murren et al. 2015; Scheiner et al. 2015). If the environmental cue is a feature of the social environment, however, phenotypically plastic developmental responses can, by shifting the composition of the population, modify the cue. In doing so, an irreversible plastic response may compromise the reliability of the social cue as a predictor of future environmental conditions, leading to potentially complex feedbacks between phenotypic plasticity and fitness.

The social environment is known to have far-reaching effects on the development and fitness of different phenotypes. In diverse taxa, variation in social environment during ontogeny alters irreversible life-history phenotypes in adulthood (Vandenbergh 1969; Kennedy and Brown 1970; Fullerton and Cowley 1971; Drickamer 1974; Rodd et al. 1997; Baddaloo and Clulow 1981; Lutnesky and Adkins 2003; Magellan et al. 2005; Kasumovic and Andrade 2006; Walling et al. 2007; Magellan and Magurran 2009; Kasumovic and Brooks 2011). For example, in several species juvenile males reared in the presence of a high density of adult males delay maturation and reach a larger size at maturity than juveniles reared in the presence of a low density of adult males (Kolluru and Reznick 1996; Magellan and Magurran 2009; Kasumovic et al. 2011). Juvenile females also respond to their social environment, accelerating maturation when exposed to a high density of adult males (Vandenbergh 1969; Kennedy and Brown 1970; Fullerton

and Cowley 1971; Lutnesky and Adkins 2003). In contrast, cockroaches (*Diploptera punctata*) exhibit the opposite trend (Holbrook and Schal 1998). These studies hypothesize that an individual's social environment during development directly impacts the age and/or size at which that individual matures. Despite ample empirical evidence that social cues can affect an individual's developmental pathway, we do not have a theoretical basis for understanding when selection should favor plastic developmental strategies that use social cues and, further, whether certain types of social information are more reliable cues than others.

As a first theoretical step, a recent verbal model defined socially cued anticipatory plasticity (SCAP) as a maturation strategy under which developmental plasticity based on social cues might be expected to evolve (Kasumovic and Brooks 2011). The goal of the SCAP verbal model was to articulate when juveniles should use social cues to guide development, as they try to predict the adult phenotype that will best match the environment that they will encounter on maturation. A SCAP strategy is expected to evolve when (1) the social cue during development reliably predicts the environment at maturation, (2) the social cue is perceptible on a time frame that allows individuals to predict which phenotype will be adaptive, and (3) SCAP individuals using these social cues have higher fitness than individuals that do not use social cues. In practice, identifying the conditions under which socially cued phenotypic plasticity might evolve is complicated by the fact that plastic responses to social cues can change the social environment.

Socially cued plasticity has, to date, primarily been examined in the context of social learning, where individuals can copy the behavior of others (Boyd and Richerson 1988*a*, 1988*b*; Henrich and Boyd 1998; Giraldeau et al. 2002; Laland 2004; Heyes 2012; Kendal et al. 2018). Previous work has found that individuals should use social learning when they are uncertain about which phenotype is favored or when the cost of a wrong choice is high. Theory has also shown that social learning is favored at intermediate rates of environmental change, while nonsocial individual learning is favored when the environment changes rapidly (Boyd and Richerson 1988*a*, 1988*b*; Rogers 1988; Feldman et al. 1996; Henrich and Boyd 1998). More recent models have also included genetically determined phenotypes and shown that such genetic strategies evolve when the environment is relatively constant (Wakano et al. 2004; Aoki et al. 2005). These studies also suggest that social learning is adaptive only when some individuals in the population sample the environment directly, and therefore social learning can never fix completely (Boyd and Richerson 1988*a*, 1988*b*; Rogers 1988; Feldman et al. 1996; Henrich and Boyd 1998; Wakano et al. 2004; Aoki et al. 2005). However, because this work is largely behavioral, strategies are usually reversible; thus, this work does not identify whether

or when SCAP could evolve. Furthermore, the majority of existing social learning theory has focused on the case where individuals learn from a single other model individual (Feldman et al. 1996; Wakano et al. 2004; Aoki et al. 2005; Aoki and Feldman 2014). Studies that have considered cases where an individual can learn from more than one model have found a greater benefit to social learning (King and Cowlishaw 2007; Enquist et al. 2010), but this work has not examined whether socially cued plasticity can evolve when individuals use population-level cues.

Here, we develop an individual-based simulation model to identify whether and when socially cued plasticity can evolve. We situate individuals in an environment that temporally oscillates between favoring one of two adult phenotypes, and we track the evolution of traits that dictate whether an individual matures according to socially cued plasticity. We find that under a narrow range of conditions (namely, when strong selection acts on survival), socially cued plasticity evolves and is adaptive. Furthermore and counterintuitively, this strategy is most effective when plasticity is costly. This work extends (1) phenotypic plasticity theory by considering a case where individuals use the social environment to cue development of alternative adult phenotypes and (2) social learning theory by examining population-level social cues, nonlearned alternative strategies, and the mode of selection acting on plastic phenotypes.

Model

We consider a population of *N* haploid individuals, each characterized by two quantitative traits (described below). One of these traits determines the probability that an individual will mature using social cues. We refer to this trait as the "social" trait and denote individual *i*'s trait value as S_i ($0 \leq S_i \leq 1$). Each day, individuals age, some die, and then adults produce offspring. We will describe each of these steps in detail below. We consider overlapping generations because the social cue derives from adults but is perceived by juveniles, and therefore both must be present together. Throughout the article, we will refer to the maturation rule that an individual uses to develop as the individual's strategy and the adult morph (*A* vs. *B*) as its phenotype. All simulation code is available at https://github.com/langeec/socially-cued-plasticity and Zenodo (Lange 2020).

Aging/Maturation

Each iteration, all individuals age by 1 day, and then individuals who are of "maturation age," which we denote by a_m, mature as one of two adult phenotypes, which we denote *A* and *B*. These could represent different color morphs, mating types, or foraging habits, for example. Individuals commit to an adult phenotype (*A* or *B*) when they are

born. Each individual has two quantitative genetic traits: a social trait (S_i) and a genetic trait (G_i). The strategy an individual uses to determine its maturation phenotype is determined by its trait value at the social locus such that, with probability S_i, it matures using social cues ("socially cued plasticity") and, with probability $(1 - S_i)$, it chooses a phenotype via an alternative strategy. We primarily modeled the social trait as a continuous quantitative trait because there is evidence that individuals differ quantitatively in their propensities to use social information (Mesoudi et al. 2016), but see appendix D (apps. A–D are available online) for cases where the social trait is binary. Because we wanted to understand when an informed decision using social cues would outperform an uninformed decision, the majority of our analyses consider a bet-hedging alternative strategy that comprises individuals adopting a phenotype randomly ("random plasticity"). However, we also consider alternative strategies where the choice of phenotype is genetically based or a consequence of stochastic phenotype switching (SPS). The genetic trait, G_i, is relevant only for these latter cases and will be described where it is relevant below.

An individual using socially cued plasticity surveys the mature adults and then commits to whichever phenotype is more common among them. An individual using random plasticity chooses phenotype A or B with equal probability. An individual using the genetic mixed strategy matures as phenotype A with probability G_i and as phenotype B with probability $(1 - G_i)$. An individual using the SPS strategy inherits their parental phenotype with probability G_i and the alternate phenotype with probability $(1 - G_i)$.

Selection

The environment favors one phenotype over the other in a temporally oscillating manner. Previous theory has suggested that temporally, rather than spatially, varying selection is more likely to promote the evolution of plasticity (Levins 1963; Moran 1992), and furthermore selection pressures are known to fluctuate temporally in natural populations (Siepielski et al. 2009). In our model, selection switches from favoring phenotype A to favoring phenotype B (and vice versa) every P days (we refer to P as the "period of selection"). More information about the strength of selection, which we denote by s, is given in the relevant sections below. We also consider asymmetric selection by defining phenotype-specific selection coefficients, s_A and s_B, which, respectively, define the strength of selection favoring each phenotype, and asymmetric periods of selection, P_A and P_B, which, respectively, define the duration over which each phenotype is favored.

To evaluate how the mode of selection affects evolution of socially cued plasticity, we incorporate phenotype-dependent fitness into an individual's life cycle in one of two ways. In the first, which we call the "survival model," selection acts on an individual's survival probability; in the second, which we call the "fecundity model," it acts on an individual's fecundity (details below).

Survival

Each day, n_d individuals die. The probability that the ith individual survives depends on this quantity and, in the survival model, on its phenotype. Survival probability decreases with increasing number of deaths, n_d, using a Moran-like process (Moran 1958). In the fecundity model, the individuals that die each day are chosen randomly, but in the survival model, their likelihood of mortality depends on their phenotype and on any potential costs associated with plasticity. Specifically, the likelihood that individual i is selected to die is increased by a factor of $1 + s$ if that individual is expressing the nonfavored phenotype. In addition, individual i also experiences a fitness cost associated with plasticity (regardless of whether it matured using social cues), which we denote $C_{v,i}$. This cost is equal to

$$C_{v,i} = \frac{1}{1 - c_v \cdot S_i}, \tag{1}$$

where c_v denotes the strength of survival costs associated with plasticity (ranges from 0 to 1) and S_i denotes individual i's trait value. The fitness cost for an individual increases with increasing trait value, S_i. These fitness components combine multiplicatively, such that individual i's probability of being selected to die in the survival model is equal to

$$D_i = \begin{cases} C_{v,i} & \text{if expressing favored phenotype,} \\ (1 + s) \cdot C_{v,i} & \text{if expressing nonfavored phenotype.} \end{cases}$$

(Note: these D_i are standardized to sum to n_d/N_{mature}, where N_{mature} is the number of mature individuals.) Under the fecundity model, there are no effects of phenotype or plasticity costs on survival, and thus $D_i = n_d/N_{mature}$ for all adults.

Reproduction

Every day, enough offspring are born to exactly replace the individuals that died (Moran 1958). Under the fecundity model, an individual's probability of parenting each of these offspring, F_i, depends on its phenotype (A or B).

Specifically, each individual of the favored phenotype is $1 + s$ times as likely as an individual of the nonfavored phenotype to produce each of the offspring. Here, individuals also suffer a fecundity cost for plasticity, $C_{f,i}$, which is equal to

$$C_{f,i} = 1 - c_f \cdot S_i, \qquad (2)$$

where c_f is the overall fecundity cost to plasticity (ranges from 0 to 1) and S_i is the value of the social trait for individual i.

These fitness components combine multiplicatively, such that individual i's probability of producing each of the offspring on a given day is equal to

$$F_i = \begin{cases} (1 + s) \cdot C_{f,i} & \text{if expressing favored phenotype,} \\ C_{f,i} & \text{if expressing nonfavored phenotype.} \end{cases}$$

(Note: these F_i are standardized to sum to 1.) Under the survival model, there are no effects of phenotype or plasticity costs on fecundity, and thus $F_i = 1/N_{\text{mature}}$ for all adults.

Mutation

Offspring inherit their parent's social and genetic trait values with mutation. Specifically, offspring i is born with trait values $S_i + \epsilon_{S,i}$ and $G_i + \epsilon_{G,i}$, where S_i and G_i denote their parental trait values at each locus and $\epsilon_{S,i}$, $\epsilon_{G,i} \sim N(0, \sigma_\mu)$; σ_μ is the mutational variance and determines the average size of mutational effects. Mutants with trait values less than 0 or greater than 1 are set to 0 and 1, respectively.

Model Runs

We initialized models with $N = 1,000$ monomorphic individuals (trait values equal to $S_i = 0$ and $G_i = 0.5$; see app. A for cases with different initial trait values). Default parameter values are shown in table 1. We ran each simulation for 10^7 days (iterations) and repeated for 50 replicate runs.

Results

We find that in a background of random plasticity, whether socially cued plasticity evolves depends on the period of environmental fluctuation, the mode and strength of selection, and costs associated with plasticity. Specifically, socially cued plasticity evolves and is adaptive (i.e., a high fraction of individuals express the favored phenotype; dis-

Table 1: Model parameter definitions and default values

Symbol	Description	Default
a_m	Age at which individuals mature	100
c_v	Survival cost of plasticity	0–.1
c_f	Fecundity cost of plasticity	0–.1
n_d	Number of individuals that die each day	5
N	Population size	1,000
s	Strength of selection	0–1
σ_μ	Mutational variance	.001
P	Period of environmental change	10^2–10^6

cussed later) when selection is strong ($s = 0.5$) and acts on survival, when the period of environmental fluctuation is large, and when plasticity is costly (figs. 1c, 2c).

When strong selection acts on survival, the cue (the frequency of the A phenotype) fluctuates more predictably as the environment switches between favoring A and favoring B (fig. 1c). When A is favored, the frequency of the A phenotype is often high, and when B is favored, the frequency of the A phenotype is often low. Here, many more individuals with the disfavored phenotype die, causing the frequency of the favored phenotype to increase rapidly. Consequently, when the selective regime switches, the composition of the adult population shifts toward containing more of the newly favored phenotype. Once this shift causes those individuals to comprise more than 50% of the population, individuals using socially cued plasticity will mature to express the newly favored phenotype. When the period is long enough that fluctuations in environment occur between generations, this results in a majority of the population expressing the optimal phenotype (fig. 3c). When selection is weaker ($s = 0.1$ or $s = 0.05$), however, the difference in survival of alternative phenotypes is not strong enough to cause variation in the social cue to reliably follow the environmental fluctuations. Therefore, socially cued plasticity is not adaptive when selection is weak (figs. 1a, 1b, 2a, 2b, 3a, 3b).

In contrast, when selection acts on fecundity, socially cued plasticity is not adaptive (figs. 1d–1f, 2, 3). Here, individuals of the favored phenotype are more likely to produce offspring. However, these offspring are equally likely to mature as either adult phenotype (at least prior to any evolution at the S-trait). Therefore, periodic environmental selection does not lead to temporal fluctuations in the frequency of the A phenotype (see colored curves in fig. 1d–1f). In contrast to when selection acts on survival, here the social cue is not a reliable predictor of the environment, and consequently there is no predictable trait evolution (fig. 2a–2c). Thus, the population never comprises many more adapted individuals than it would if individuals adopted phenotypes at random (fig. 3).
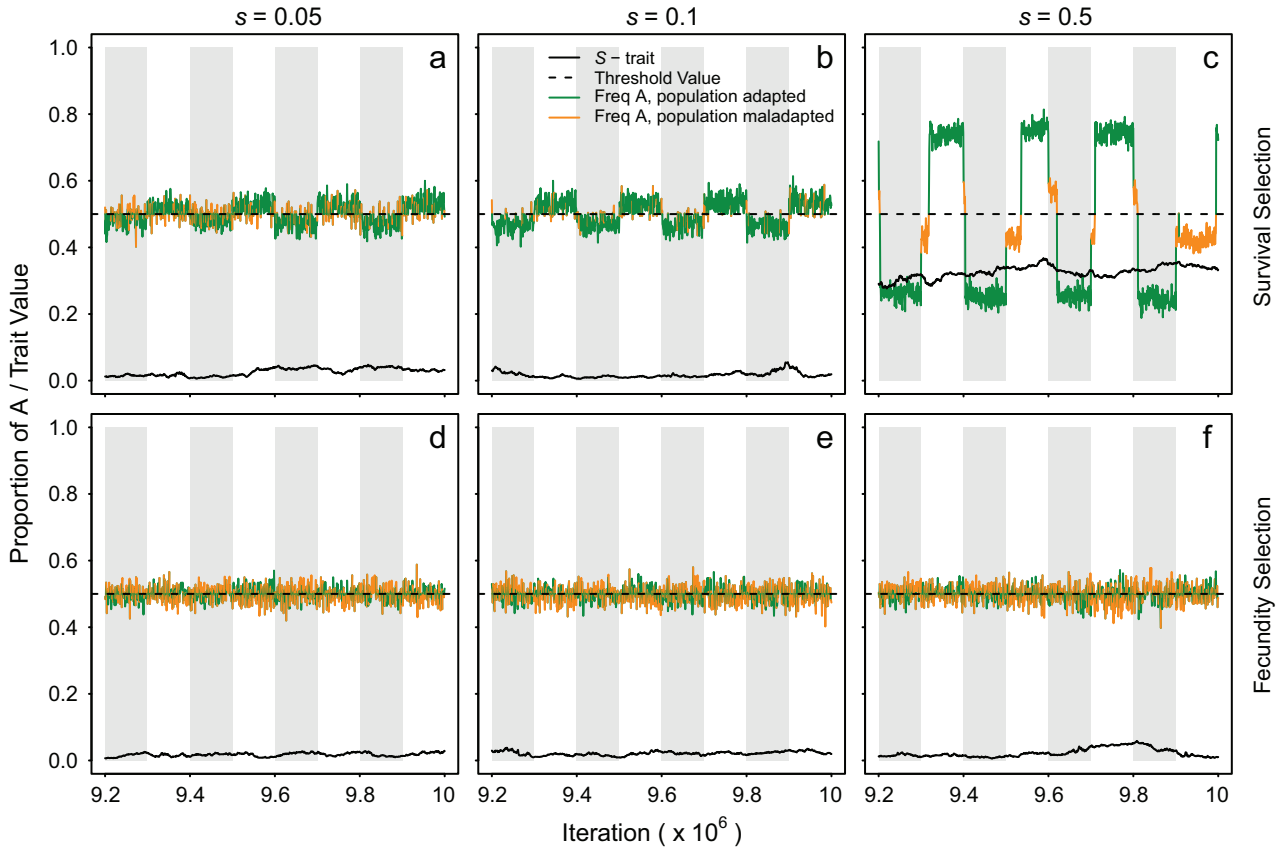
Figure 1: Sample model runs when selection operates on survival (*top*) or fecundity (*bottom*). The colored line shows the fraction of the population expressing the *A* phenotype (line is colored green when the majority of the population is expressing the favored phenotype and orange when the majority of the population is expressing the nonfavored phenotype). The black solid line shows the population average *S*-trait. White regions indicate when the *A* phenotype is favored; gray regions indicate when the *B* phenotype is favored. Columns correspond to different strengths of selection. In each panel, the last $8P$ days are shown for runs that comprise 10^7 days in total. Models were run with $N = 1{,}000$ individuals with initial trait value $S_i = 0$ and $P = 10^5$ days; $c_v = 0.1$ in the top panels, and $c_f = 0.1$ in the bottom panels. Refer to table 1 for default parameter values.

Surprisingly, we find that when costs associated with plasticity are lower, adaptive evolution of socially cued plasticity is limited (figs. 4, 5). Without costs, social plasticity still evolves (fig. 2*d*–2*f*), but the fraction of individuals expressing the favored phenotype is reduced (compare blue lines in the top and bottom rows of fig. 3). This is because without costs there is no direct selection against indefinite upward *S*-trait evolution. Once enough individuals mature using adaptive plasticity, the fluctuations in the proportion of the *A* phenotype will remain always above or always below 0.5, and thus the most common phenotype will no longer track environmental selection (fig. 4). Once this happens, all individuals using socially cued plasticity will express whichever phenotype is more common, even when the alternative is better. From here, further evolutionary dynamics at the *S*-trait are largely governed by drift, and

individuals tend to be maladapted as often as they are adapted (unless the *S*-trait drifts to lower levels). Thus, once *S*-trait values evolve to high levels without costs, individuals express the correct phenotype less often then they do when plasticity is costly (fig. 5). When selection acts on fecundity, socially cued plasticity, which did not evolve when it was costly because it was not adaptive (fig. 2*a*–2*c*), now evolves via drift (figs. 2*d*–2*f*, 4*d*–4*f*) but remains nonadaptive (fig. 3*d*–3*f*).

When the environment changes often (e.g., a short period of selection), maturing using social cues is maladaptive with or without costs (figs. 2, 3). This is because individuals must commit to a phenotype when they are born, and if the environment is changing rapidly relative to generation time, using socially cued plasticity can lead to the wrong phenotype. Thus, when the period is short and the
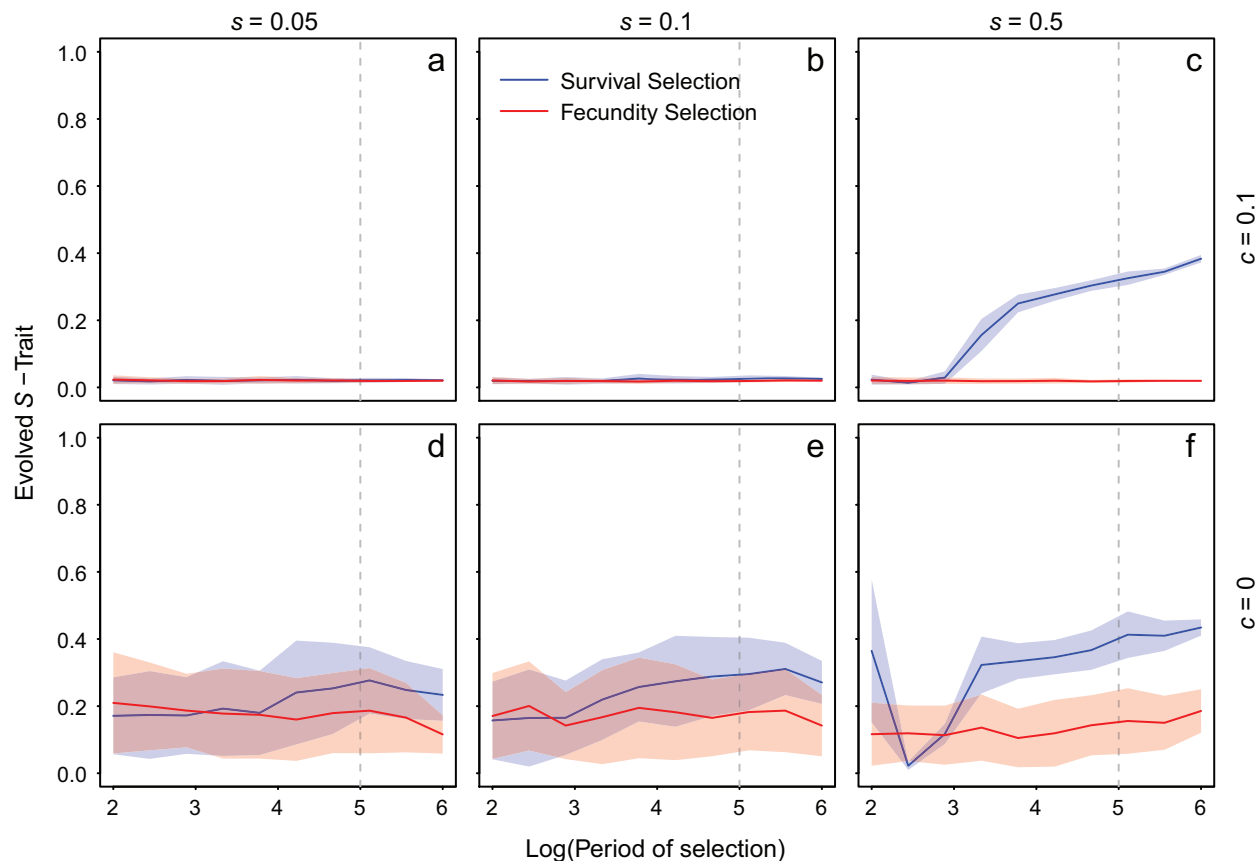
Figure 2: Evolved *S*-trait values after 10^7 days of evolution as a function of the period of environmental change for the survival model (blue) and fecundity model (red). Small values on the horizontal axis represent environmental fluctuations occurring within a generation, while large values correspond to fluctuations occurring over many generations. Columns correspond to different strengths of selection (*s*). In the top row plasticity is costly ($c_v = 0.1$ in survival model; $c_f = 0.1$ in fecundity model), whereas in the bottom row plasticity is not costly ($c_v = 0$; $c_f = 0$). Lines and shaded regions show means and standard deviations across 50 replicate runs. Vertical dashed lines correspond to the periods shown in figures 1 and 4. Other parameter values are as in figure 1.

environment changes within a generation, socially cued plasticity can be maladaptive, and consequently lower trait values are favored. However, this effect disappears when the environment changes so rapidly that any "planning" is essentially irrelevant. We observe higher and more variable evolved trait values for the shortest periods of environmental change (left side of blue curve in fig. 2*f*). The high variability across these runs suggests that evolution here was largely occurring via drift. Furthermore, the fraction of the population expressing the optimal phenotype was not different from our null expectation of 0.5 (fig. 3), indicating that although socially cued plasticity sometimes evolves, it is not adaptive.

These results are robust to starting conditions as long as there is a cost to plasticity (compare fig. 2 with fig. A1 and fig. 3 with fig. A2; figs. A1–A5, B1, B2, C1, D1, D2

are available online). When there is no cost to plasticity, however, populations that have initially high levels of plasticity will tend to remain high because in the absence of costs, drift is the only process that will lower the frequency of adaptive plasticity. Qualitative phenotype dynamics at the selected locus are insensitive to initial conditions. Findings are also qualitatively similar when only a single individual dies per day ($n_d = 1$; fig. A3).

In summary, if selection is strong and acts on survival, evolution can lead to a state where a substantial fraction of individuals are able, via socially cued plasticity, to rapidly respond to changes in the environment. When this happens, socially cued plastic individuals tend to express the favored phenotype more often than the disfavored one (fig. 3). Furthermore, costs to plasticity help keep levels of socially cued adaptive plasticity in a range where plasticity
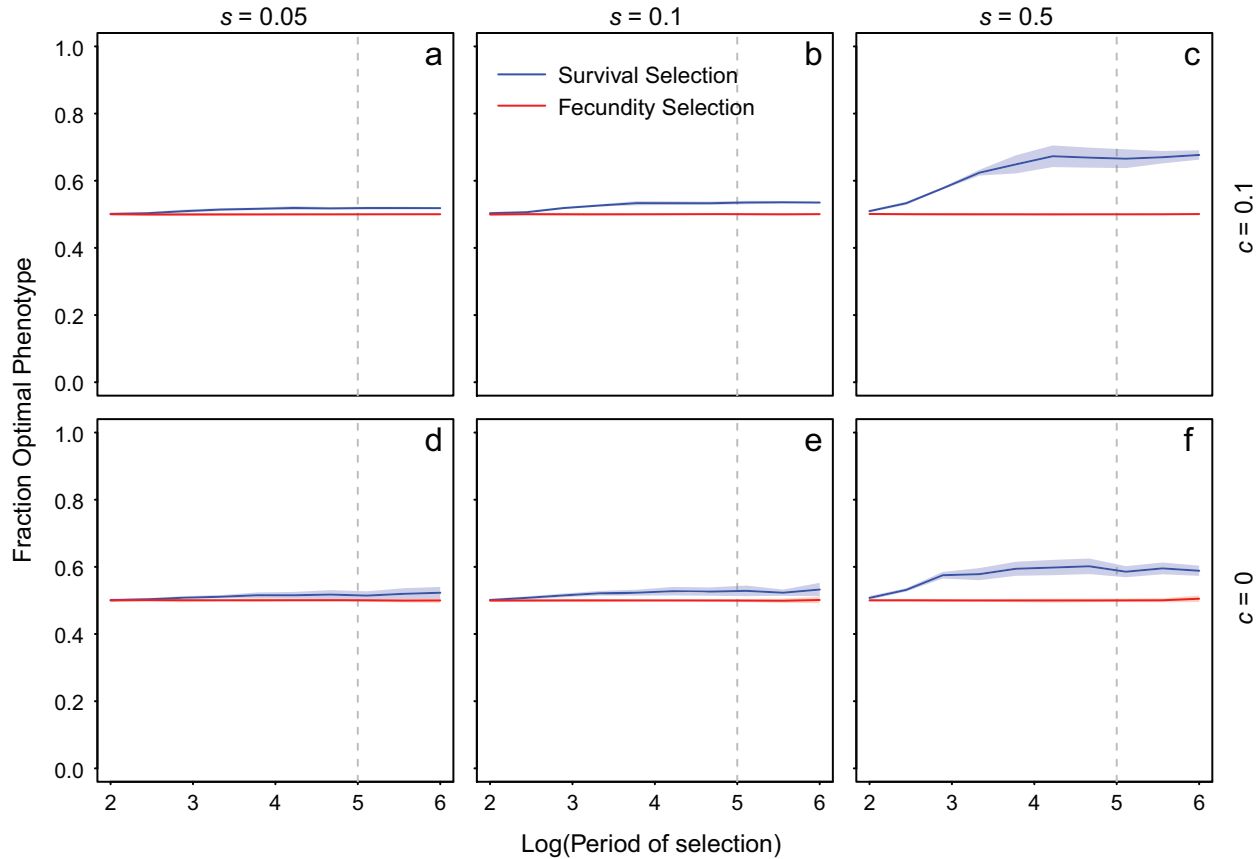
Figure 3: Fraction of the population adopting the favored phenotype as a function of the period of environmental change for the survival model (blue) and the fecundity model (red). To calculate the fraction of the population expressing the optimal phenotype, we computed the mean fraction of individuals exhibiting the optimal phenotype over the last $8P$ days of the model run. A population that is unable to respond to environmental change will be adapted half of the time, and thus 0.5 corresponds to a worst-case outcome. See figure 2 for descriptions of panels. Other parameter values are as in figure 1.

remains adaptive (fig. 5). In contrast, if selection is weak or if it operates on fecundity, populations are unable to respond to changes in the environment. In this case, all individuals that mature via socially cued plasticity remain fixed for one or the other phenotype, thus spending half their time in a maladapted state.

Alternative Strategies

Provided selection acts on survival, socially cued adaptive plasticity evolves most easily in a background where individuals that do not mature via socially cued plasticity choose phenotypes at random (fig. 6a, 6e). In contrast, when evolving in a background of individuals with genetically determined phenotypes, socially cued plasticity still evolves, but to lower levels (fig. 6a). Here, evolution at the G-trait enables a direct evolutionary response to environmental change and thereby lowers benefits to socially cued

plasticity (figs. 6c, A4b, A4e, A4h). Finally, socially cued plasticity does not evolve at all in a background of SPS (figs. 6a, A4c, A4f) unless the mutation rate is very low (fig. A4i). Under SPS, individuals evolve to produce offspring of both phenotypes when the period of environmental change is short or offspring primarily of their own phenotype when the period is long. This strategy is highly effective at eliciting rapid responses to environment change, and consequently a socially cued plasticity strategy cannot compete.

When mutation rates are low (e.g., 10^{-4}), evolution at the G-trait cannot keep pace with the rate of environmental change. Consequently, the G-trait evolves to 0.5, and all models (random plasticity, genetic, and SPS) effectively become the same, at which point the S-trait evolves to intermediate trait values (fig. A4g–A4i). When selection acts on fecundity, socially cued plasticity does not evolve, regardless of the alternative strategy (figs. 6b, A5).
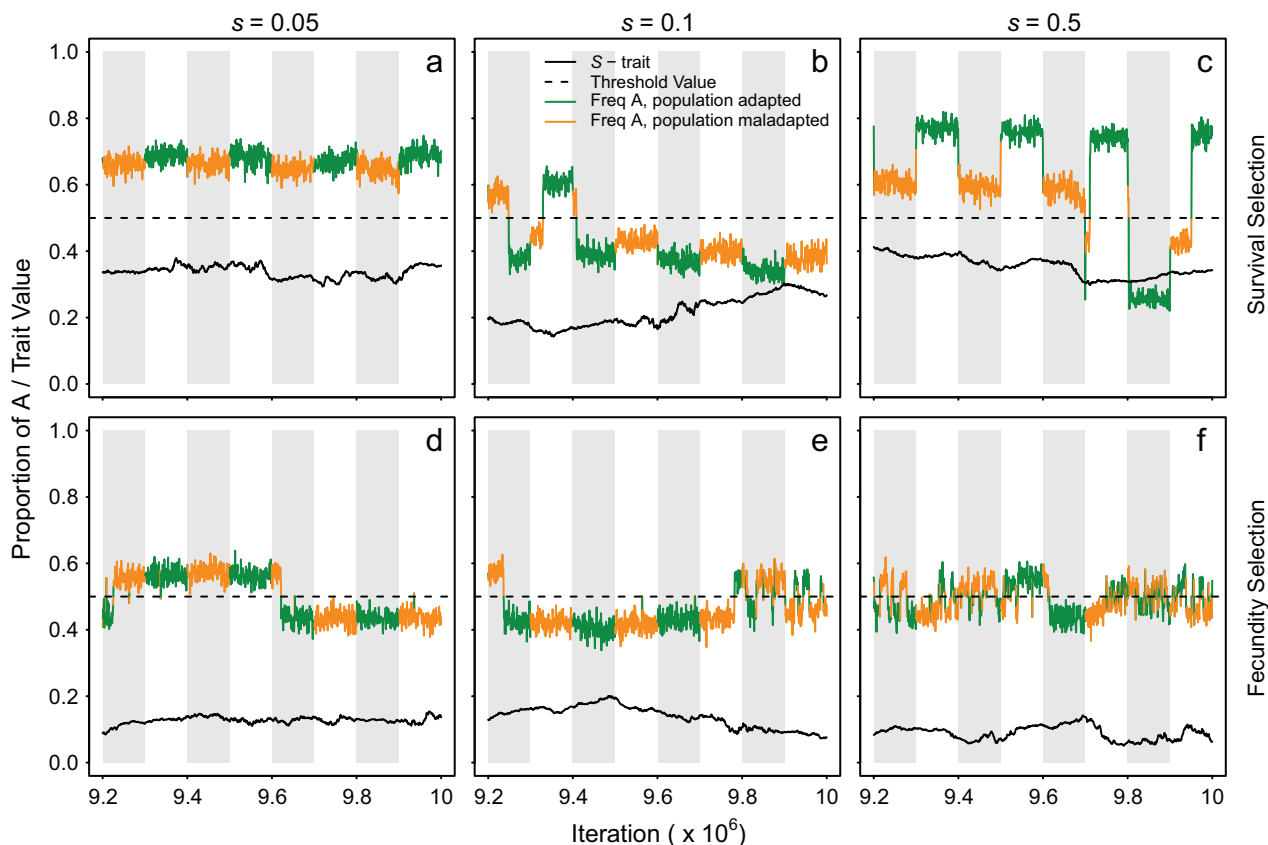
Figure 4: Sample model runs when plasticity is not costly ($c_v = 0$; $c_f = 0$). Panels and other parameter values are as in figure 1.

Asymmetric Selection

When selection is asymmetric, such that the A phenotype is more strongly favored (fig. B1) or favored for longer (fig. B2), the extent to which socially cued plasticity evolves depends, as it did in the symmetrical case, on the period of environmental fluctuation, selection strength, mode of selection, and costs associated with plasticity. Socially cued plasticity still evolves when selection on survival is asymmetric, provided that this asymmetry in selection strength is not too great. As in the symmetric case, when selection acts on fecundity, socially cued plasticity does not evolve. See appendix B for more information.

Maturation Age

The age at which an individual matures alters the timing between when a socially cued individual uses social cues to adopt a phenotype and when the phenotype is expressed at adulthood. Age at maturation also affects the turnover rate of the adults that comprise the social cue that juveniles use. Therefore, we assessed the effect of variation in

maturation age, a_m, and find that our results are robust to changes. We find that evolutionary dynamics of adaptive socially cued plasticity are relatively insensitive to how long it takes for individuals to mature (fig. C1). See appendix C for more details.

Obligate Strategies

When expression at the S-trait was binary ($S = 0$ vs. $S = 1$) such that individuals either never ($S = 0$) or always ($S = 1$) use socially cued plasticity, we find that the evolution of adaptive socially cued plasticity depends critically on the mutation rate. When the mutation rate is high, evolutionary dynamics are qualitatively similar to when the S-trait was quantitative (figs. D1a, D1d, D2e, D2f). However, when the mutation rate is intermediate and the period is long, socially cued plasticity evolves to near fixation and is adaptive when selection acts on survival and when selection acts on fecundity (figs. D1b, D1e, D2c, D2d). When the mutation rate is low, dynamics are similar when selection acts on survival, except for
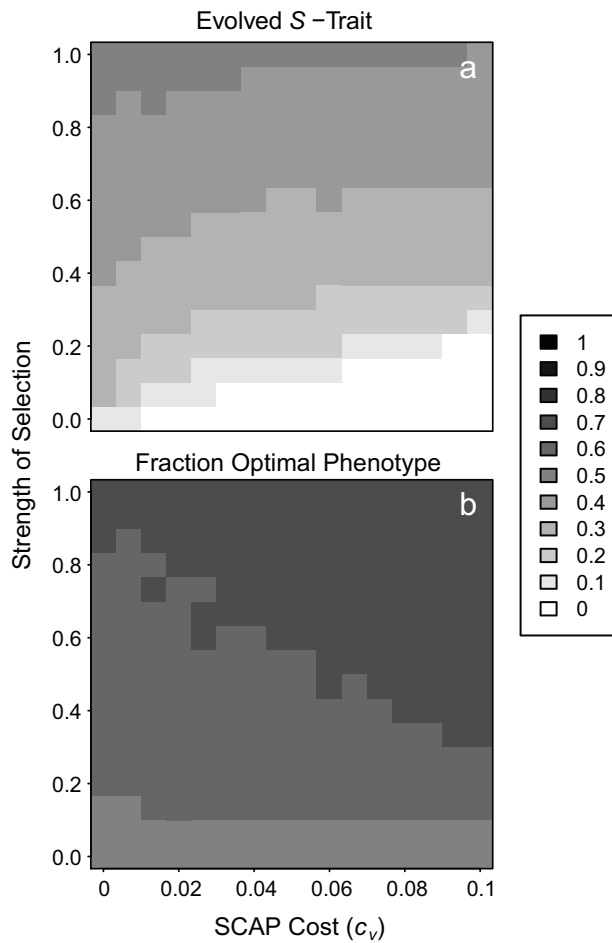
Figure 5: Evolved *S*-trait values (*a*) and fraction of the population adopting the favored phenotype (*b*) over a range of strengths of selection and costs to plasticity for the survival model. Values for fraction optimal phenotype were calculated as in figure 3. Other parameter values are as in figure 1. The fecundity model is not shown because no appreciable evolution occurs (but see fig. A3). SCAP = socially cued anticipatory plasticity.

a range of intermediate period lengths when the population never switches between alternative phenotypes, so although socially cued plasticity evolves, it is not adapative (figs. D1*c*, D1*f*, D2*c*). Socially cued plasticity does not evolve when selection acts on fecundity if the mutation rate is low (figs. D1*c*, D1*f*, D2*f*). See appendix D for further information.

Discussion

Phenotypic plasticity is widespread (Scheiner 1993; Pigliucci 2001, 2005; West-Eberhard 2003), but little is known about how plasticity evolves when plastic responses can change the very environmental conditions to which they are a re-

sponse. For example, an intriguing verbal model proposed that it might be adaptive for juveniles to use their social environment as a cue to trigger development of their adult phenotype (Kasumovic and Brooks 2011). This SCAP strategy would seem most plausible in situations where the social environment an individual experiences as a juvenile predicts the social environment that it will encounter as an adult. Here, we used simulation models to test this idea. Specifically, we considered an environment that fluctuated between favoring one of two phenotypes and asked whether socially cued plasticity was adaptive. We found that it was adaptive, but only under a narrow range of conditions.

Previous work has suggested that a cue must reliably predict optimal phenotypes in order for the evolution of irreversible plasticity (Levins 1963; Lively 1986; Moran 1992; Tufto 2000; Scheiner and Holt 2012; Scheiner 2013; Botero et al. 2015) or social learning (Boyd and Richerson 1988*b*; Feldman et al. 1996; Wakano et al. 2004; Aoki et al. 2005) to be adaptive. In our model, fluctuations in the social cue accurately reflect fluctuations in the selective environment only under specific conditions. Specifically, we found that socially cued plasticity can be adaptive when strong selection acts on survival, as opposed to fecundity, and when plasticity is costly. If these conditions were not met, the social cue was not a reliable indicator of the environmental condition, and thus, even if individuals used socially cued plasticity, it was not adaptive. This finding parallels a similar finding that selection on life span, rather than fecundity, can promote the evolution of horizontal transmission of symbionts (Brown and Akçay 2019). Combined, these findings suggest that selection on survival may promote the evolution of a range of phenotypes that selection on fecundity does not.

Socially cued plasticity was also more likely to evolve when the period of environmental fluctuation was long enough that the environment remained constant across multiple generations. This aligns with previous theoretical work on abiotic environments where developmental plasticity is expected to evolve when environmental variation is "coarse grained," such that environmental changes occur between, rather than within, generations (Levins 1963; Orzack 1985; Lively 1986; Moran 1992; Scheiner and Holt 2012; Botero et al. 2015). We also found that in a background comprising a genetically mixed strategy, intermediate periods of environmental fluctuation were most conducive to the evolution of socially cued plasticity. This conclusion parallels findings from studies of social learning (Wakano et al. 2004; Aoki et al. 2005) and thus reinforces the principle that for a variety of cues, both abiotic and social, understanding the pattern of environmental variation is crucial in determining when plasticity might evolve.

We also found that socially cued plasticity was most adaptive when it was costly. Without costs, the benefits
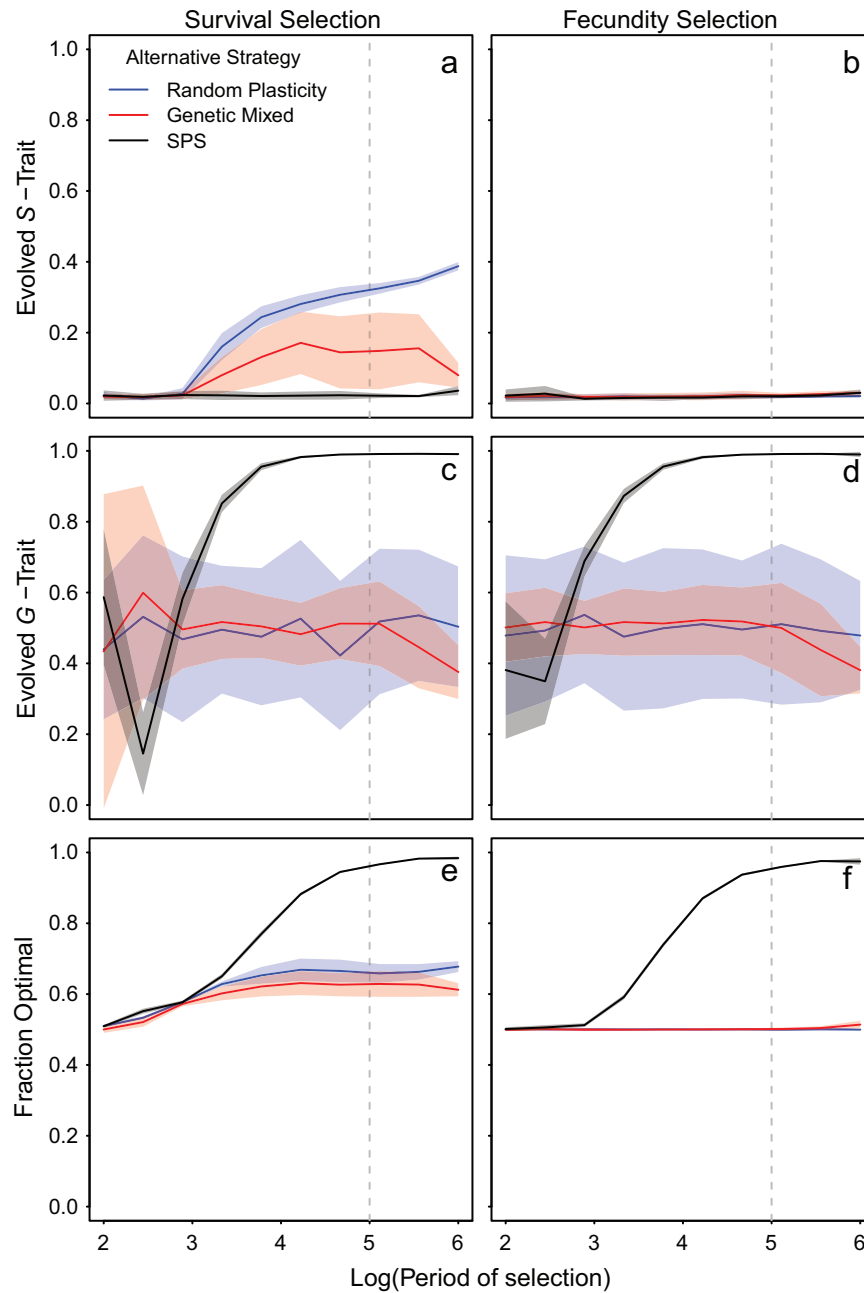
Figure 6: Evolved *S*-trait (*top row*), evolved *G*-trait (*middle row*), and fraction of the population adopting the favored phenotype (*bottom row*) for cases where the alternative strategy was either random plasticity (blue), genetically determined phenotypes (red), or stochastic phenotype switching (SPS; black). In all cases, there was a cost to plasticity ($c_v = 0.1$, *left panels*; $c_f = 0.1$, *right panels*). Values for fraction optimal phenotype were calculated as in figure 3. Vertical dashed lines correspond to the periods shown in figures A4 and A5. Other parameter values are as in figure 1.

of socially cued plasticity disappear when it becomes too common because when most individuals use social cues, the composition of adult phenotypes (the cue) becomes largely unlinked from environmental fluctuations, and

thus the population becomes largely fixed for a single adult phenotype. Costs associated with higher plasticity help mitigate this by creating a selection pressure against plasticity when it no longer conveys benefits. Therefore,

socially cued plasticity is most beneficial under the conditions where intuitively it seems least likely to evolve (DeWitt et al. 1998; Auld et al. 2010). That a single process can promote the evolution of social learning while simultaneously limiting the number of social learners is also well documented in the cultural evolution literature. For example, studies of social learning have found that benefits to using social cues depend on how many individuals directly sample the environment rather than use social cues (Boyd and Richerson 1988*b*; Rogers 1988; Giraldeau et al. 2002; Laland 2004). This mirrors our finding that enough individuals in the population must respond to environmental factors directly in order for socially cued plasticity to remain beneficial.

In our model, socially cued plasticity is a conformist strategy (an individual using social cues adopts the most common phenotype in the population). Some theoretical models suggest that using conformity as a socially cued strategy promotes the evolution of social learning in a variety of environments (Boyd and Richerson 1988*b*; Henrich and Boyd 1998). However, more recent studies suggest that these environmental conditions are limited (Kameda and Nakanishi 2002; Eriksson et al. 2007; Nakahashi 2007; Wakano and Aoki 2007) and that social conformity can lead to population collapse (Whitehead and Richerson 2009). For example, when individual learning is costly, more individuals use social learning, but the level of social conformity is lower (Kameda and Nakanishi 2002). When there are fewer individuals using social learning, social conformity evolves to a high level. This is analogous to our finding that costs to plasticity, by limiting the proportion of the population using social cues, can promote the efficacy of socially cued plasticity. There are other ways individuals could use socially plastic cues (e.g., adopting a rare phenotype or adopting the phenotype of a dominant individual; Laland 2004), and future modeling efforts could examine how these modes of social information use might affect the evolution of SCAP.

Our model examines whether socially cued plasticity can evolve when phenotypic plasticity is irreversible. The nature of age and size at maturity and many other phenotypic traits (e.g., many color polymorphisms, defensive structures) is that they are irreversible; a single individual cannot mature at different ages or sizes. Other well-known examples of phenotypic plasticity are also irreversible (e.g., helmets in *Daphnia* [Grant and Bayly 1981] or trichomes in plants [Agrawal 1999]). Our model seeks to explain when individuals with traits that are fixed at maturity might evolve to use social cues to alter these common irreversible phenotypes. There are also flexible traits, including behavioral phenotypes, where an individual's propensity toward a certain phenotype is influenced by its social environment. The evolution of such socially cued but reversible plasticity may require different environmental conditions. For example, previous work suggests that reversible phenotypes may evolve when the timescale of environmental variation is short, and therefore SCAP with reversible phenotypes may evolve under shorter periods of environmental change (Botero et al. 2015). However, costs are also expected to affect the evolution of reversible socially cued plasticity and may promote its evolution at period lengths not predicted by models of plasticity with abiotic cues. Future theoretical work could examine how outcomes might differ for reversible plasticity.

We have used a haploid model of inheritance to facilitate implementation and interpretation. This is not outside the realm of biological realism. For many species, differences in life-history morphs are Y-linked and thus are essentially haploid (Kallman et al. 1973; Borowsky 1987*b*; Wirtz Ocana et al. 2014). For example, in swordtails (*Xiphophorus variatus*) males inherit size and mating behavior via a single Y-linked locus. Furthermore, there is evidence that male swordtails use social cues and irreversible plasticity in the development of life-history phenotypes (Borowsky 1973, 1978, 1987*a*; Sohn 1977). There are also numerous examples of diploids with irreversible plastic life-history phenotypes (e.g., age and size at maturation; Drickamer 1974; Baddaloo and Clulow 1981; Walling et al. 2007). Differences between modes of inheritance could affect the reliability of the social cue and, thus, the evolution of socially cued plasticity, and it would be worthwhile for future studies to examine the effect of genetic architecture.

In natural populations, social environment can be the genesis of selection pressure (e.g., frequency-dependent selection) and/or a cue to the direction of selection. We considered the latter case where selective pressures are external and social environment provides a cue as to which phenotypes are likely to be favored (Rodd et al. 1997; Kasumovic and Brooks 2011; Diaz Pauli and Heino 2013). However, understanding how socially cued plasticity could evolve when selection is frequency dependent is another interesting potential extension.

Future empirical studies could also test predictions of our model. We suggest that socially cued plasticity should evolve when the social environment is a reliable cue of external selective forces. While we know that species respond to social cues to alter development, we do not know whether social cues predict which phenotype or phenotypes are likely to be favored by the extrinsic environment. Determining how social structure fluctuates with temporally varying selection in natural populations is a fundamental prerequisite for socially cued plasticity. Furthermore, empirical tests to examine whether individuals that use social cues to alter their phenotypes achieve higher fitness would be invaluable.

Conclusions

Whether irreversible socially cued plasticity can evolve depends critically on the mode, strength, and duration of fluctuating selection. Our theory shows that socially cued plasticity can evolve, but only in cases where selection is strong and acts on survival differences between adult phenotypes. Socially cued plasticity is adaptive over a larger range of conditions when plasticity is costly. These conclusions suggest that SCAP for irreversible phenotypes is probably not a general phenomenon and a qualitatively different process than evolution of plasticity when cues are abiotic. Therefore, socially cued plasticity is not a special case of abiotic cued plasticity but instead a fundamentally different process.

Acknowledgments

Statement of Authorship

All authors contributed to the conceptualization and design of the study. E.C.L. and L.K.M. implemented the model, analyzed the results, and prepared the manuscript. All authors provided feedback on results and edits to the manuscript.

Data and Code Availability

All simulation code is available at https://github.com /langeec/socially-cued-plasticity and Zenodo (Lange 2020).

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Associate Editor: Erol Akçay
Editor: Russell Bonduriansky

"The Prairie Dog at Home." From the review of *The Standard Natural History* (*The American Naturalist,* 1884, 18:403–404).