



The information provided by the absence of cues: insights from Bayesian models of within and transgenerational plasticity

Judy A. Stamps¹ · Alison M. Bell²

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Abstract

Empirical studies of phenotypic plasticity often use an experimental design in which the subjects in experimental treatments are exposed to cues, while the subjects in control treatments are maintained in the absence of those cues. However, researchers have virtually ignored the question of what, if any, information might be provided to subjects by the absence of the cues in control treatments. We apply basic principles of information-updating to several experimental protocols used to study phenotypic plasticity in response to cues from predators to show why the reliability of the information provided by the absence of those cues in a control treatment might vary as a function of the subjects' experiences in the experimental treatment. We then analyze Bayesian models designed to mimic fully factorial experimental studies of trans and within-generational plasticity, in which parents, offspring, both or neither are exposed to cues from predators, and the information-states of the offspring in the different groups are compared at the end of the experiment. The models predict that the pattern of differences in offspring information-state across the four treatment groups will vary among experiments, depending on the reliability of the information provided by the control treatment, and the parent's initial estimate of the value of the state (the parental Prior). We suggest that variation among experiments in the reliability of the information provided by the absence of particular cues in the control treatment may be a general phenomenon, and that Bayesian approaches can be useful in interpreting the results of such experiments.

Keywords Developmental plasticity · Parental effects · Within-generational plasticity · WGP · Transgenerational plasticity · TGP · Socially cued plasticity · Updating · Social cues

Introduction

Empiricists studying phenotypic plasticity frequently use experimental designs in which the subjects are randomly divided into two treatment groups. In one group (the experimental treatment), the subjects are exposed to certain stimuli over the course of development, while in the other group (the

control treatment), the subjects are reared in the absence of those stimuli. At the end of the experiment, differences between the phenotypes of the experimental and the treatment groups are used to assess phenotypic plasticity. For instance, many investigators have used this protocol to study phenotypic plasticity in response to stimuli from predators. Versions of this protocol have been used to study within-generational plasticity (WGP: e.g., when exposure to stimuli within an individual's lifetime affects the development of its traits (e.g., Relyea 2001), transgenerational plasticity (TGP: when exposure to stimuli for parents affects the development of traits in their offspring (e.g., Storm and Lima 2010), and recently, trans- and within-generational plasticity (TWP: when exposure to stimuli in the parental and in the offspring generation affects the development of traits in the offspring (e.g., Stein et al. 2018) (see Table 1 for terms).

An implicit assumption in such experiments is that the stimuli used in the treatment group provide the experimental subjects with information about some aspects of the external

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✉ Judy A. Stamps
jastamps@ucdavis.edu

¹ Evolution and Ecology, University of California, Davis, Davis, CA, USA

² Evolution, Ecology and Behavior, University of Illinois at Urbana-Champaign, Urbana, IL, USA

Table 1 Terms

Estimate: an organism's current estimate of the value of a state of the environment. In Bayesian models, this estimate is provided by the mean of the organism's current prior or posterior distribution
Likelihood (likelihood function): a distribution specifying the conditional probability that a particular experience will occur, given each of the possible values of a state of the environment
NN: An experimental design in which neither parents nor offspring are exposed to cues from predators
NP: An experimental design in which parents are not exposed to cues from predators, offspring are exposed to those cues
Parental Prior: A distribution indicating the parent's assessment of the probability of all possible values of a state of the environment at the beginning of an experimental study of TGP or TWP. The mean of a parental prior indicates the parent's estimate of the value of the state; the variance of a parental prior indicates the parent's level of confidence in that estimate
PN: An experimental design in which parents are exposed to cues from predators, offspring are not
PP: An experimental design in which both parents and offspring are exposed to cues from predators
State of the environment: A variable in the external environment (e.g., predator density). Particular cues (e.g., a certain concentration of chemicals produced by a predator) can be used to update an organism's estimate of particular states of the environment
TGP: Transgenerational plasticity
TWP: Within and transgenerational plasticity
WGP: Within-generational plasticity

environment. For instance, exposure to a certain concentration of kairomones from a particular species of predator might provide prey individuals with information about the density of that type of predator. In addition, it is assumed that the only reason that the stimuli from predators affect development is because they provide information. This is in contrast to other types of experiences which induce changes in development, because they have lasting effects on somatic states, instead of, or in addition to, providing information about the external environment (see Engqvist and Reinhold 2016; Nettle and Bateson 2015; Nettle et al. 2013; Sultan 2017). Examples of inductive experiences with direct effects on a developing organism's somatic state include food deprivation in animals, shade in plants, and extreme temperatures in either. Conversely, examples of information-only inductive experiences include stimuli from predators, conspecifics, or competitors. As Nettle and Bateson (2015) point out, if an inductive cue is information-only, then one can imagine a single loss-of-function mutation that completely abolishes an individual's ability to detect that cue, but which leaves the developing individual otherwise unaffected.

However, while it is widely assumed that phenotypic plasticity may occur in response to exposure to information-only cues, empiricists and theoreticians alike have virtually ignored two questions: 1) what, if any, information might be provided to the same organisms if they are raised in the absence of those cues, and 2) how information from ancestors (i.e., provided by genes or parental effects) and/or a subject's own experiences earlier in life) would affect the results of such experiments. To answer both questions, we need to consider how organisms integrate information from different sources and different times to update their estimates of conditions in their environment. Because Bayesian updating is in principle the optimal way to combine information

to estimate variables in the external environment (Lange and Dukas 2009; McNamara et al. 2006), in recent years, a number of authors have used Bayesian models to study developmental plasticity in response to various types of experiences (English et al. 2016; Fawcett and Frankenhuis 2015; Fischer et al. 2014; Frankenhuis and Panchanathan 2011; Panchanathan and Frankenhuis 2016; Stamps and Krishnan 2014a, b, 2017), review in Stamps and Frankenhuis (2016). Thus far, Bayesian models of development have focused on WGP, and investigated how information from its ancestors (in the form of an initial information-state modelled by a prior distribution) combines with the information provided by a series of experiences over an individual's lifetime to affect its information-state and/or its phenotype. Here, we expand the scope of inquiry to consider information-updating in the context of TWP, and use Bayesian approaches to model situations in which a parent's information-state at the onset of an experiment (provided by a parental prior distribution) combines with information from parental experiences and information from offspring experiences to affect the offspring's estimates of conditions in the external environment.

To take advantage of the rich theoretical and empirical literature on the effects of stimuli from predators on phenotypic plasticity, we designed our models to mimic an experiment in which parents, offspring, both or neither are either exposed to cues from predators (P treatments), or not exposed to those cues (N treatments). That is, we model fully factorial experiments with four treatment groups: both parents and offspring are exposed to predator cues (PP), parents but not offspring are exposed to predator cues (PN), offspring but not parents are exposed to predator cues (NP) and neither parents nor offspring are exposed to predator cues (NN), where the first letter indicates the parent's experience, and the second letter indicates the offspring's

experience. Examples of experiments which have used this design to investigate the combined effects of cues from predators within and across generations on offspring phenotypes include Agrawal et al. (1999), Beaty et al. (2016), Donelan and Trussell (2018), Luquet and Tardieu (2016), and Stein et al. (2018).

For each treatment group, we determined the offspring's estimate of the value of a variable in the external environment (e.g., its estimate of predator density) at the end of the experiment. That is, we focused on the information-states of the offspring in the four treatment groups, not their phenotypes. Given our goal of analyzing the information provided by the absence of particular cues, there were several advantages to this approach. First, information-based models that predict phenotypic traits typically rely on highly simplified assumptions about information-updating to make the models mathematically tractable. For instance, virtually, all of the recent information-based models that predict the evolution of developmental systems or trait values assume that the environmental state that is being estimated can only take on one of two discrete values, e.g., a habitat that is either type A or type B (English et al. 2016; Fischer et al. 2014; McNamara et al. 2016; Panchanathan and Frankenhuysen 2016). As we show below, analysis of the information provided by the absence of particular cues requires more complicated models in which the environmental state that is being estimated can take on a range of different values. Second, this approach allows us to trace how and why different assumptions about the information provided by the absence of particular cues would affect offspring estimates of the value of environmental variables. This is more difficult in models which predict phenotypes, because of the host of assumptions about variables other than information-updating (e.g., details of a species' life-history, developmental constraints, the optimal shape of functional relationships between estimates and trait values, environmental factors besides the one of interest) that are required to predict the trait values that will be expressed by individuals as a function of their experiences earlier in life.

Finally, in experimental studies of phenotypic plasticity in response to information-only cues, differences among treatment groups in information-state set a lower limit for inter-group differences in phenotypes. This is because the researchers who conduct this type of experiment typically randomly assign subjects to their respective treatments and thereafter maintain them under the same conditions, except for the presence or absence of the cues of interest in the experimental and control treatments. In this situation, if the subjects in two or more treatment groups ended up with the same estimate of the value of a state of the environment, there would be no reason to expect them to exhibit different trait values related to that state. Hence, although differences among treatment groups in their estimates of

the value of a state need not map directly onto differences among those groups in their phenotypes, the absence of differences among treatment groups in their estimates would be expected to result in a lack of differences among them in their phenotypes.

Assumptions about the information provided by the presence or absence of particular experiences and the parent's prior distribution

To appreciate the information that might be provided to experimental subjects by the absence of cues from predators in an N treatment, we need to consider some basic principles of information-based models of phenotypic plasticity. We describe these here in non-technical terms; readers interested in more details are directed to the Online Resource, and the references cited therein.

Any model of information-updating begins by specifying three things: the 'state of the environment' that individuals are attempting to estimate, the information about that state that is provided by a particular experience, and the subject's estimate of the value of that state before it has that experience. In Bayesian models, the information about a given state that is provided by a particular experience is modelled by the 'likelihood function' for that experience, and a subject's estimate of the value of that state before it is exposed to the experience is modelled by its prior distribution.

The first step in modelling empirical studies of plasticity in response to cues from predators is to identify a state of the environment for which the exposure to cues from predators in the experimental treatment indicates a value that is different from the value indicated by the absence of those cues in the control treatment. This is because if conditions in the experimental treatment and conditions in the control treatment indicate similar values of a state (e.g., if the likelihood functions for the subjects' experiences in the P and the N treatments had similar means), we would expect the phenotypes of the subjects in the two treatments to have similar means. Then, after such a state has been identified, we need to compare the reliability of the information provided by exposure to the cues in the P treatment with the reliability of the information provided by the absence of those cues in the N treatment (in Bayesian models, the reliability of information provided by a given experience is indicated by the variance of the likelihood function for that experience, see Online Fig. 1).

As a first approximation, when animals are exposed to stimuli from predators, it may be useful to assume that the state of the environment that they are estimating is 'risk of predation' (Agrawal et al. 1999; Donelan and Trussell 2018; Seiter and Schausberger 2015; Stein et al. 2018). However,

in nature, animals may be exposed to many different cues from predators, and this variety has encouraged investigators to use different cues and protocols in their experiments. As a result, we must delve deeper to identify states of the environment for which exposure to the cues in a P treatment would indicate different values than the absence of those cues in an N treatment.

For instance, in nature, aquatic animals may be exposed to olfactory cues (kairomones) from predators for much to all of their lifetimes. Based on these observations, empiricists have demonstrated that being reared from birth to maturity in the presence of such cues affects the development of a variety of antipredator traits. In such cases, it is often assumed that the subjects in the P treatment are using the concentration of kairomones from predators to estimate the value of the state ‘predator density’ (Ferrari et al. 2010; Gilbert 2011; Luttbegg et al. 2020; Roux et al. 2014; Shaffery and Relyea 2016). This assumption is supported by observations that antipredator behavioral and morphological traits often increase as a function of concentrations of kairomones from predators in a dose-dependent manner (Gilbert 2011; Loose and Dawidowicz 1994; Miyakawa et al. 2015; Roux et al. 2014; Shaffery and Relyea 2016; Van Buskirk and Arioli 2002). In such cases, it would be reasonable to assume that the conditions in the P and N treatments indicate different values of predator density. For instance, if prolonged exposure to a high concentration of kairomones in the P treatment indicated that predator density was high, prolonged exposure to no kairomones in the N treatment would indicate that predator density was low, since in the latter case, the concentration never exceeded the preys’ threshold for detection. In addition, it would be reasonable to assume that the reliability of the information provided by the continued absence of kairomones in the N treatment would be similar to the reliability of the information provided by their continued presence in the P treatment.

In other situations, animals may be briefly, but repeatedly, exposed to cues from predators over the course of ontogeny. Thus, some populations of guppies (*Poecilia reticulata*) live in streams which also contain piscine predators (*Crenicichla* sp.) (Magurran 2005), such that in nature, a juvenile guppy might detect this predator swimming nearby on multiple occasions prior to maturity. Experiments designed to mimic brief, repeated encounters of guppies with this predator (e.g., 5 min exposure to visual and chemical cues from *Crenicichla* at randomly chosen times of day, 5 days a week) have shown that this type of experience can affect the development of both body size and relative brain size in guppies (Reddon et al. 2018). In such cases, it is assumed that repeated, brief exposures to predator stimuli provide the prey with information about the state ‘encounter rate’ (e.g., Luttbegg and Trussell 2013). In this situation, it would be reasonable to assume that if repeated exposures to visual cues from a predator in

the P treatment indicated with a certain level of reliability that the encounter rate was high, then the absence of these cues in the N treatment would indicate, with a similar level of reliability, that the encounter rate was low.

In contrast, other types of experiences involving stimuli from predators are unlikely to occur many times over the life of an individual. Examples include a near-escape from a direct attack by a predator. If an attack by a predator is likely to have a lethal outcome, then a given individual would be unlikely to have and survive many such attacks over the course of its lifetime. In addition, we would expect per-capita rates of successful attacks on prey individuals by predators to be low at a given locality, since moderate-to-high rates of lethal attacks by predators can lead to local extinction (Armstrong et al. 2006; Festa-Bianchet et al. 2006). However, empirical studies have shown that even one near-escape from a predator can have enduring effects on behavioral and other traits. Thus, in nature, the probability that an insect pollinator will be attacked by a spider lurking in a flower is low (Morse 1986), but even one such attack can change the pollinator’s subsequent behavior (Dukas and Morse 2003). Similarly, a single unprotected exposure of a rat to a cat can have long-lasting effects on the rat’s brain and behavior (Adamec et al. 2006).

However, if the cue in a P treatment consisted of a single near-escape from a predator over an extended (e.g., a 4-month) period, then the presence of this cue in the P treatment and the absence of this cue in the N treatment would indicate similar values of some states of the environment relevant to predation risk. For instance, the preys’ experiences in both treatments would indicate that predator density was low. Similarly, the preys’ experiences in both treatments would indicate comparably low values of another state, ‘encounter rate per day’, based on the subjects’ history of 0.008 encounters/day in the P treatment, versus 0.000 encounters/day in the N treatment.

However, a single near-escape from a predator in the P treatment over an extended period of time could provide the individuals in the P and the N treatments with different estimates of another state related to predation risk: the probability that a predator that poses a direct, potentially lethal threat to the experimental subject lives in the area. In that case, the attack in the P treatment might indicate that such a predator lived in the area, whereas the absence of any attacks in the N treatment might indicate that it did not. This interpretation would be reasonable in species in which ambush predators sometimes do and sometimes do not overlap spatially with a given prey individual, but when they do, the predators are site-faithful for periods as long or longer than the lifetime of a prey individual. Moreover, in this case, the reliability of the information provided by the subject’s experiences in the P and the N treatment might differ considerably. That is, a single near-escape might indicate, with a relatively high

level of reliability, that a threatening predator was in residence. In contrast, the absence of attacks in the N treatment would not be expected to provide an equally reliable indication that a threatening predator did not live in the area. This is because not being attacked by a predator over a 4-month period might indicate that the predator was absent, but that same experience would also be consistent with a situation in which the predator did live in the area, but the subject simply had not encountered it yet. Bayesian analyses of other rare events (e.g., estimating whether or not earthquakes occur at a given location) have shown that although an extended period in which no events occurred may provide some information about the state of the environment, the reliability of this information is typically low (Mangel and Beder 1985; Quigley et al. 2007; Styron and Hetland 2014). Hence, in this situation, it seems reasonable to assume that the reliability of the information provided by the cues in the P treatment would be higher than the reliability of the cues provided by the absence of those cues in the N treatment.

Based on these considerations, we designed and analyzed two sets of Bayesian models of the effects of cues for parents and offspring on offspring estimates of states of the environment. In both sets, we assumed that reliable information about a state of the environment related to risk of predation was provided by the cues in the P treatment. However, for the first set of models, we assumed that the information provided by the cues in the P treatment and the absence of those cues in the N treatment was equally reliable, whereas for the second set, we assumed that the information provided by the cues in the P treatment was much more reliable than the information provided by their absence in the N treatment. Then, we used both sets of models to predict the offspring estimates which we would expect in the NN, NP, PN, and PP treatment groups in experimental studies of TWP.

In addition, for each set of models, we asked whether differences in the information-state of the parents at the onset of the experiment would affect the results. Currently, most empiricists studying TWP focus on the information provided by the cue, which is equivalent to assuming that parents have no information about the value of a state at the beginning of the experiment. We instead assume that parents might begin an experiment with an initial estimate of the value of the state of interest, and model this estimate by the mean of the parental Prior distribution. In theory, parental Priors could vary among experiments, e.g., among populations as a result of different information provided by genes or inherited epigenetic factors, or among different samples from the same population, e.g., as a function of different experiences the parents had before they were placed in their respective treatments. Hence, strong effects of parental Priors on the results of either set of models would suggest that more attention be paid to this factor in theoretical and empirical studies of TWP.

Methods

Background information on the Bayesian models of development used in the current article is described in the Online Resource. We assumed that each parent began with a prior distribution (Prior), based on information from their ancestors and any experiences they had before the experiment, where the mean of the parental Prior indicates the parent's initial estimate of the value of a state, and the variance of the parental Prior indicates the parent's confidence in that estimate. We did not consider parental Priors with low variance, since in that situation, even the most reliable cues have little to no effect on estimates of the value of the state. Preliminary analyses indicated that for Priors with intermediate-to-high variance, the variance of the Priors had no qualitative effects on the patterns generated by the models. Hence, in the text, we present results based on three informative Priors, with different means (0.1, 0.5, and 0.9) and the same variance (0.04). We also analyzed models in which the parental Prior provided no information about the state (a uniform distribution with mean = 0.5, variance = 0.0833), but since the results for this Prior were qualitatively similar to those for the informative Prior with a mean of 0.5, they were not considered further.

We assumed that cues from the predator in the P treatment were always informative, and used beta functions with shapes modelled by $\alpha > \beta$ to indicate the cumulative likelihood functions for the conditions in the P treatments (Online Fig. 1a). We assumed that parents and offspring in the P treatments were exposed to the same cues for the same period of time, so we used the same cumulative likelihood functions for the P treatments for parents and offspring.

Based on the expectation that different experimental protocols might result in differences in the relative reliability of the information provided by conditions in the P and the N treatments (see above), we analyzed two sets of models which differed with respect to their assumptions about the reliability of the information provided by the N treatment. In the first set (N* models), the information provided by the P treatment and the information provided by the N treatment were equally reliable. In this case, the cumulative likelihood function for the N treatment was the mirror-image of the cumulative likelihood function for the P treatment. For instance, if all of the experiences in the P treatment resulted in a cumulative likelihood function that indicated that the value of the state of the environment was likely to be high (e.g., with a shape modelled by $\alpha = 8, \beta = 1$), conditions in the N treatment had a cumulative likelihood function which indicated that the value of the state was likely to be low (e.g., with a shape modelled by $\alpha = 1, \beta = 8$) (Online Fig. 1b).

In the second set of models (N-), the information provided by the N treatment was less reliable than the

information provided by the P treatment. We first analyzed this situation by assuming that conditions in the P treatment were either highly reliable (likelihood with a shape modelled by $\alpha=8$, $\beta=1$) or weakly reliable (likelihood modelled by $\alpha=2$, $\beta=1$), while conditions in N provided no information about the state (i.e., the cumulative likelihood function for the N treatment had a uniform distribution ($\alpha=1$, $\beta=1$) (Online Fig. 1c). We also analyzed models in which the information provided by the N treatment was weakly reliable, but much less reliable than the information provided by the P treatment. The results of these analyses were qualitatively the same as those of models in which the information provided by the P treatment was highly reliable and conditions in N were non-informative, so in the interest of brevity, they are not considered further.

For all of the models, we computed the offspring estimates of the value of the state at the end of their respective treatments, where each estimate was the mean of the offspring posterior distribution at the end of the experiment.

Results

General patterns

The differences between the offspring estimates for the four treatment groups depended on the reliability of the cues to which the subjects were exposed. In both the N* and the N- models, the differences among the estimates for the four treatment groups were more pronounced when the cues in the P treatment were highly reliable than when the cues in the P treatment were less reliable (compare Fig. 1a versus 1b, and Fig. 2a versus 2b).

For all parental Priors and likelihood functions, the offspring estimate for the NP group was the same as the offspring estimate for the PN group (Figs. 1 and 2). This result indicates that additional assumptions would be required to predict different offspring estimates for the NP and PN treatment groups.

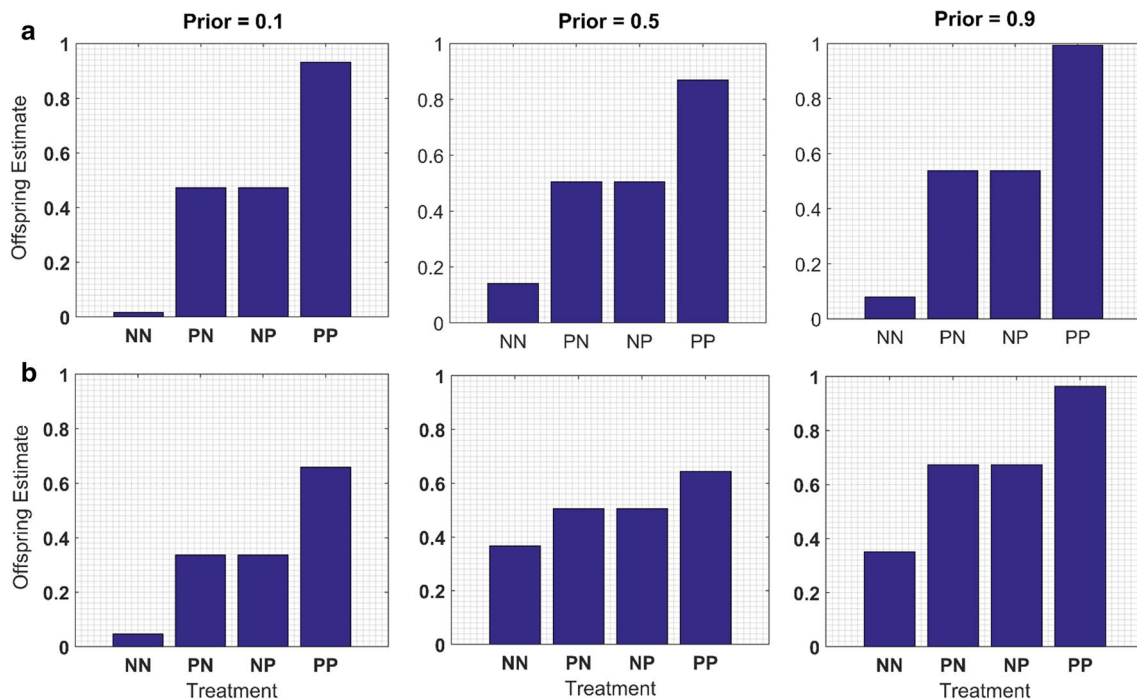


Fig. 1 N* models; different cue reliabilities. P treatment=exposure to cues from a predator; N treatment=no cues from predators. First letter=parental treatment, second letter=offspring treatment. In these models, exposure to cues in the P treatment and the absence of cues in the N treatment provide equally reliable information, such that the cumulative likelihood functions for the P and N treatments are mirror-images of one another. **a** Exposure to cues in the P treatment indicates with high reliability that the state of the environment is likely to be high (likelihood modelled by $\alpha=8$, $\beta=1$); absence of cues in the N treatment indicates with high reliability that the state

of the environment is likely to be low (likelihood modelled by $\alpha=1$, $\beta=8$). **b** Exposure to the cues in the P treatment indicates with low reliability that the state of the environment is likely to be high (likelihood modelled by $\alpha=2$, $\beta=1$); absence of cues in the N treatment indicates with low reliability that the state of the environment is likely to be low (likelihood modelled by $\alpha=1$, $\beta=2$). Predicted offspring estimates of the value of a state of the environment (e.g., estimates of predator density) for each of the four treatment groups (NN, PN, NP, and PP) are indicated for parental Priors with three different means (0.1, 0.5, and 0.9) and the same variance (0.04)

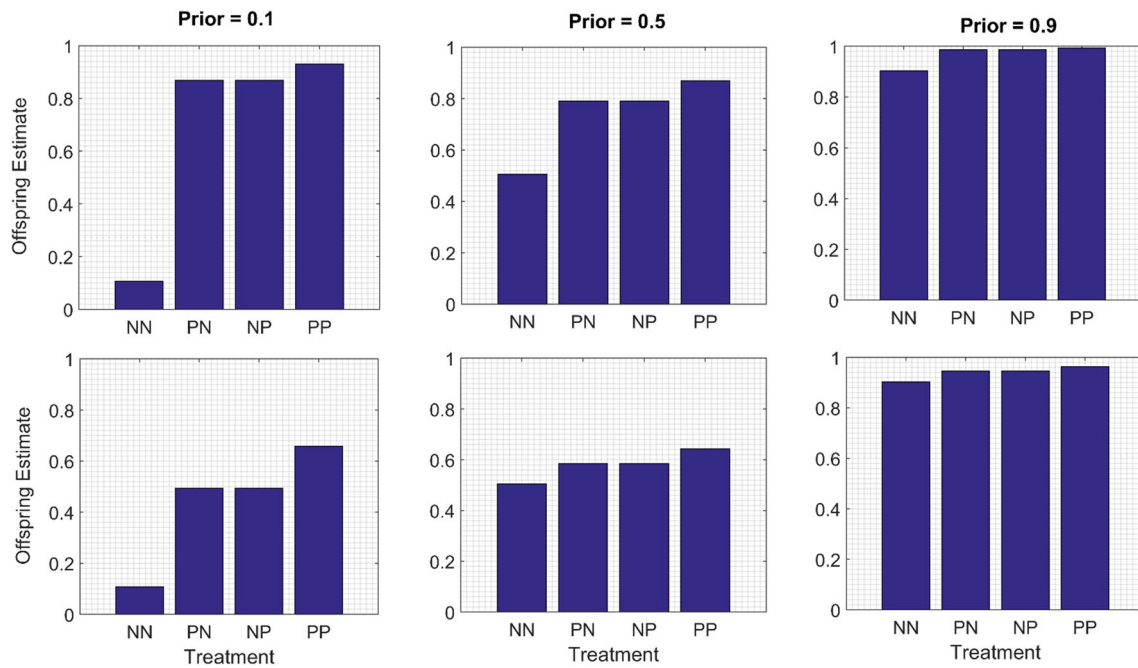


Fig. 2 N- models; different cue reliabilities. In "N- models", conditions in the N treatment provide less reliable information than conditions in the P treatment. **a** Information provided by the P treatment is highly reliable, modelled by a cumulative likelihood function with a shape indicated by $\alpha=8$, $\beta=1$; information provided by the N treat-

ment is unreliable, and is modelled by a uniform distribution ($\alpha=1$, $\beta=1$). **b** Information in the P treatment is weakly reliable (likelihood modelled by $\alpha=2$, $\beta=1$; information provided by the N treatment is modelled by a uniform distribution ($\alpha=1$, $\beta=1$))

Reliability of information in the N treatment: N* versus N- models

N* models

When conditions in the N treatment provided information as reliable as that provided by the cues in the P treatment (N* models), different parental Priors generated similar 'step up' patterns, in which the offspring estimates for the NN and PP groups differed from one another, and the estimates for the PN and NP groups were intermediate between them (Fig. 1). The similarity of the patterns for different parental Priors occurred because when the information provided by both the P and N treatments was reliable, the cumulative effects of those experiences across two generations were strong enough to outweigh most effects of the parental Priors on the results. The intermediate estimates for the NP and PN treatments occurred because when the likelihood function for the parental experience was the mirror-image of the likelihood function for the offspring experience, the most extensive area of overlap between the two likelihood functions (i.e., the values of the state which were possible given both experiences) occurred for intermediate values of the state (compare Online Fig. 1a, b). The differences among the treatment groups in offspring estimates were most pronounced when the cues in both the P and N treatments were

highly reliable (Fig. 1a), but were also apparent even when both cues were weakly reliable (Fig. 1b).

N- models

When conditions in the N treatment provided less reliable information than those in the P treatment (N- models), the patterns generated were strongly dependent on the parental Priors (Fig. 2). For any parental Prior, the estimates for the NN group at the end of the experiment were the same as the estimates of the state indicated by the parental Prior at the beginning of the experiment. This is because we assumed that conditions in the N treatment provided no information about the state. In this situation, the parent's initial estimate of the value of the state was maintained across both generations.

Across different parental Priors, the difference between the offspring estimates for the NN and the PP groups depended on the extent to which the initial estimate of the value of the state provided by the parental Prior differed from the value of the state indicated by the cues in the P treatment. Recall our assumption that the cues from the predator in the P treatment indicated that the value of the state of the environment is high. In that case, the difference between the offspring estimates for the NN and PP groups was most pronounced when the parental Prior and the cues

in the P treatment indicated very different values of the state, i.e., when the parental Prior was low (Prior = 0.1, Fig. 2). Conversely, the difference between the offspring estimates for the NN and PP groups was minimal when the parental Prior was high (Prior = 0.9), i.e., when the parental Prior and the cue indicated similar values of the state. These results were due to a basic feature of Bayesian updating, the ‘discrepancy rule’. The discrepancy rule specifies that changes in an individual’s estimate of the value of a state of the environment as a result of a given experience will be positively related to the discrepancy between the estimate of the value provided by its prior distribution and the estimate of the value provided by the likelihood function for that experience (see Stamps et al. 2018; Stamps and Frankenhuis 2016)).

When the parental Priors had low-to-intermediate mean values, the N- models generated a ‘jump-up’ pattern, in which the offspring estimates for the NN group were different from those of the other three groups (PN, NP, and PP), whose estimates were similar, but not identical, to one another (Fig. 2). The jump-up pattern occurred because in Bayesian updating, the effects of sequential exposures to the same cue on an individual’s estimate of the value of the state of the environment are non-additive: initial exposure to a cue results in more change in an individual’s estimate than do subsequent exposures to the same cue (Stamps and Krishnan 2014a, b). As a result, one dose of exposure to the cue in a P treatment (in either the parental or the offspring generation) generated estimates of the value of the state of the environment that approached the estimate generated by two doses to the cue (in both the parent and the offspring generation).

Comparison of the results of N- models with different levels of reliability for the P treatments indicates that the difference in the reliability of the information provided by the P versus the N treatments was largely responsible for the patterns observed. Although the jump-up pattern was still detectable when the information provided by the P treatment was only slightly more reliable than that for the N treatment (Fig. 2b), the differences among the four treatment groups in their estimates were less pronounced in this situation. These results suggest that jump-up patterns would be most strongly expressed when the cue in the P treatment provided highly reliable information about a state of the environment, but the absence of the cue in the N treatment provided little or no information about the same state.

Discussion

Our results indicate that assumptions about the information that is provided by the absence of particular cues in experimental studies of phenotypic plasticity can have major effects on differences among treatment groups in the information-states of the subjects at the end of those experiments.

We explored this topic using models designed to mimic fully factorial empirical studies of TWP (trans- and within-generational plasticity) with four treatment groups: both parents and offspring are exposed to cues from predators (PP), neither are exposed to those cues (NN), or one of the two are exposed to those cues (NP, NP). We then asked whether, and if so how, different assumptions about the information provided by the control (N) treatments in this type of experiment would affect offspring estimates of the value of a state of the environment at the end of the experiment. Based on previous empirical and theoretical studies of the effects of different types of cues from predators on phenotypic plasticity (see “Introduction”), we assumed that exposure to cues in the P treatment always provides reliable information about the state of the environment (e.g., predator density). We then asked whether and how differences in the reliability of the information provided by the absence of cues from predators in the N treatment would affect the differences among the four treatments in offspring estimates of the state of the environment.

When the absence of cues from predators in the control (N) treatment provided information as reliable as the presence of those cues in the P treatment (N* models), we observed a ‘step up’ pattern, in which the offspring’ final estimates of a state related to predation were most different for the NN and PP groups, and the estimates for the PN and NP groups were intermediate between them. These results were robust in the face of variation in parental Priors and cue reliability. These patterns fit our intuitive sense of what we might expect to see in experimental studies of TWP, e.g., the effects of zero, one or two ‘doses’ of exposure to the same cue on the offspring’ information-state appeared to be approximately additive.

In contrast, when the absence of cues from predators in the N treatment provided much less reliable information than the presence of those cues in the P treatment (N- models), the results were more complicated and less intuitive. In this case, the results strongly depended on the parent’s initial estimate of the value of the state of the environment, modelled here by the parental Prior. When the parent’s initial estimate of the value of the state was different from the value of the state indicated by the cues in the P treatment, we observed a ‘jump up’ pattern, in which offspring estimates for the NN treatment were different than the offspring estimates for the other three treatments (PN, NP, and PP), all of which were similar to one another. In contrast, when the parental Prior and the cues in the P treatment indicated a similar value of the state, all four treatment groups ended up with similar estimates of the state. The jump-up pattern was more strongly expressed when the cues in the P treatment were highly reliable than when they were weakly reliable.

These results suggest that to the extent that parental Priors vary among populations as a result of differences in parental

genes, inherited epigenetic factors, or grand-parental effects, the results of experiments with non-informative controls might vary as a function of the population from which the parents were collected. For instance, we would expect parents collected from populations in which a lethal predator nearly always overlaps spatially with individual prey to not exhibit much, if any, plasticity in response to an attack by that predator in the P treatment, since, in that case, the experience in the P treatment would simply confirm the estimate of the state provided by the parental Priors. In contrast, our results suggest that jump-up patterns for information-states (and possibly also phenotypes, see above) would be more likely if parents were collected from populations in which a lethal, site-faithful predator only occasionally overlapped spatially with the prey, because in the latter case, the parent's initial estimate of the probability of being attacked by that predator would be contradicted by the experience in the P treatment.

As was described in the Introduction, the N* models were designed to mimic experiments in which parents, offspring, both or neither were continuously exposed to cues such as kairomones from predators from birth to maturity. Thus, based on information-updating alone, when investigators use this protocol, we would expect antipredator trait values in the four treatment groups to differ most for the NN and PP groups, with intermediate trait values for the NP and PN groups. In turn, deviations from these patterns would suggest the need to invoke additional assumptions, including assumptions about factors other than information-updating, to explain the results.

To date, several studies of TWP have used experimental protocols that conform to those assumed in the N* models: parents and offspring exposed to the same concentration of kairomones from predators for the same period of time (birth to maturity), after which antipredator traits in the offspring are measured in four treatment groups (NN, NP, PN, and PP). In one of these, a classic study of *Daphnia cucullate*, the authors reported a step-up pattern, in which the antipredator trait values for all four treatment groups significantly differed from one another: PP > NP > PN > NN (Agrawal et al. 1999). However, other patterns have been reported in studies of a snail, *Physa acuta*, which used similar experimental designs. Thus Luquet and Turiel (2016) reported a pattern of PP, NP > PN > NN for two antipredator traits (Luquet and Turiel 2016; Turiel, unpublished data), while Beaty et al. (2016) reported that exposure to cues in parents, but not offspring, affected crush-resistance (PP, PN > NP, NN), whereas exposure to offspring, but not parents, affected antipredator behavior (PP, NP > PN, NN). Beaty et al. (2016) explained their results by suggesting that transgenerational plasticity might be more common for slow-developing traits or traits with early developmental windows (e.g., morphological traits such as crush-resistance), whereas

within-generational plasticity might be more common for behavioral or other temporally labile traits.

Thus far, only one empirical study of TWP in response to cues from predators has used a design comparable to that mimicked by the N- models. Stein et al. (2018) exposed three-spined sticklebacks (*Gasterosteus aculeatus*) to simulated attacks by a model predator. Parental males were chased once by a model sculpin for 2 min when they were caring for their young, their offspring were chased for 1 min per day for 7 days. Then, several traits, including antipredator behavior, were scored when the juveniles were 2 months old. Stein et al. (2018) were surprised to find a 'jump-up' pattern for all of the traits which they measured (NN ≠ PN, NP, PP). However, based on the results of the current study, we would expect this pattern based on information-updating alone. Recall that if the offspring in two or more treatment groups end up with the same (or very similar) estimates of a state of the environment, we would expect the offspring in those groups to express comparable values of any traits affected by those estimates. Hence, if the offspring estimates of a state followed a strong jump-up pattern, one would also expect to see a jump-pattern in trait values related to those estimates, without any need to invoke assumptions about other factors that might have affected the trait values expressed in the different treatment groups.

More generally, these results suggest that biologists studying phenotypic plasticity in response to information-only cues might want to consider the information provided by the absence as well as the presence of those cues. As was described above, for some states of the environment, the absence of particular cues may provide information as reliable as their presence, while for other states of the environment, the absence of particular cues may provide little or no information to developing organisms. These points apply to any information-only cue, not just those related to risk of predation.

For instance, experiments with insects and spiders have shown that exposing late-stage juveniles to auditory, chemical, visual, vibratory, or other stimuli from breeding adults can affect a wide range of reproductive behaviors after those juveniles mature (reviews in Dion et al. 2019; Kasumovic and Brooks 2011). It is widely assumed that one reason that cues from adults might affect behavioral development is that those cues provide juveniles with information about the density of potential mates or reproductive competitors they are likely to encounter after they mature and join the breeding population (Bailey et al. 2010; Fowler-Finn and Rodriguez 2012; Rebar et al. 2016; Stoffer and Uetz 2015). In that case, a 'control' treatment in which juveniles were reared in the absence of cues from adults might also provide reliable information about the same state of the environment, namely indicating that the density of mates or competitors was low at the current locality.

However, stimuli from breeding adults may provide juveniles with information about aspects of the local breeding environment besides density. For instance, female treehoppers (*Enchenopa binotata*) and crickets (*Ephippiger diurnus*) exposed as juveniles to the signals of highly attractive males were more selective in response to male signals after maturity than females exposed as juveniles to the signals of less attractive males (Fowler-Finn and Rodriguez 2012; Rebar et al. 2019). Similarly, female wolf spiders (*Schizocosa ocreata*) exposed as juveniles to the courtship displays of males with small leg-tufts were more receptive after maturity to males with small tufts than were females exposed as juveniles to the courtship displays of males with large tufts (Stoffer and Uetz 2016). These and similar studies suggest that arthropods might use cues from adult conspecifics prior to maturity to update their estimates of the types of mates or competitors which they were likely to encounter after maturity. However, a control treatment in which females were reared in the absence of cues from adult males would not provide any information about these states of the environment. Instead, juveniles reared in the absence of cues from adults would presumably have to rely on information from their ancestors (in Bayesian terms, their naïve priors) to estimate the types of mates or competitors which they might encounter after maturity. Hence, in experimental studies of the WGP of reproductive behavior in response to cues from adult conspecifics, a control treatment in which juveniles were reared in the absence of social cues could provide information about some states of the environment relevant to the development of adult reproductive behavior (e.g., the density of potential mates or competitors at the current locality) but not others (e.g., the distribution of different types of mates or competitors at the current locality).

Until recently, theoretical and empirical treatments comparing TGP and WGP have focused on whether they are different ways of achieving the same outcome (e.g., Bonduriansky et al. 2012; Uller 2008), the conditions under which we expect either form of plasticity to evolve (e.g., Ezard et al. 2014; Hoyle and Ezard 2012), and whether they are produced via the same or different mechanisms (e.g., Hales et al. 2017). However, theory indicates that a given organism can receive information that affects their development from a variety of sources, including their own experiences, the experiences of their parents, and their genes (Dall et al. 2015; Leimar et al. 2006; Leimar and McNamara 2015; McNamara et al. 2016), which raises intriguing questions about how information from different sources might combine to affect offspring estimates of conditions in their environment (Stamps and Frankenhuis 2016; Stamps and Krishnan 2014a). Here, we have considered one such question: how assumptions about the information provided by the absence of cues in a control group might affect the results of empirical studies of the combined effects of parental and

offspring experiences on offspring development. Our results suggest that theoreticians and empiricists alike might benefit from paying more attention to the reliability of the information provided by the absence of particular cues in studies of WGP, TGP, and TWP.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval This article does not contain any studies with human participants or animals performed by any of the authors.

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