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Maternal effects and parent–offspring conflict

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Maternal effects can provide offspring with reliable information about the environment they are likely to experience, but also offer scope for maternal manipulation of young when interests diverge between parents and offspring. To predict the impact of parent–offspring conflict, we model the evolution of maternal effects on local adaptation of young. We find that parent–offspring conflict strongly influences the stability of maternal effects; moreover, the nature of the disagreement between parents and young predicts how conflict is resolved: when mothers favor less extreme mixtures of phenotypes relative to offspring (i.e., when mothers stand to gain by hedging their bets), mothers win the conflict by providing offspring with limited amounts of information. When offspring favor overproduction of one and the same phenotype across all environments compared to mothers (e.g., when offspring favor a larger body size), neither side wins the conflict and signaling breaks down. Only when offspring favor less extreme mixtures relative to their mothers (something no current model predicts), offspring win the conflict and obtain full information about the environment. We conclude that a partial or complete breakdown of informative maternal effects will be the norm rather than the exception in the presence of parent–offspring conflict.

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Maternal effects comprise any causal influence of the environment or phenotype of the mother on the phenotype of her offspring that is not mediated by genetic transmission (Wolf and Wade 2009; Day and Bonduriansky 2011; Danchin et al. 2011). Such effects have been identified in many species, and may involve a wide variety of different mechanisms, ranging from hormonal influences (von Engelhardt and Groothuis 2011), through the transmission of antibodies (e.g., Boulinier and Staszewski 2008) and maternal provisioning of nutrients (e.g., Wells 2010), to social learning (Mesoudi et al. 2016) and even active teaching (Rapaport 2011). It is well established that maternal effects can, at least in principle, strongly influence the course of evolution within a population (Mousseau and Fox 1998; Räsänen and Kruuk 2007; Badyaev and Uller 2009; Hoyle and Ezard 2012). More recently, there has been much discussion of when and why selection might favor the evolution of such effects themselves (Kuijper et al. 2014; English et al. 2015; Kuijper and Hoyle 2015; McNamara et al. 2016; Proulx and Teotónio 2017).

Adaptive explanations of the evolution of maternal effects often suggest that they serve to provide offspring with information about the environment they are likely to encounter (Marshall and Uller 2007; Shea et al. 2011; Kuijper and Johnstone 2013; Burgess and Marshall 2014). This information allows the young to anticipate the challenges they will face and to develop an appropriate phenotypic response (Agrawal et al. 1999; Galloway and Etterson 2007; McGhee and Bell 2014; Holeski et al. 2012). For instance, offspring field crickets (*Gryllus pennsylvanicus*) born from mothers that have been exposed to predators exhibit greater antipredator immobility (Storm and Lima 2010). Other antipredator adaptations have been observed in *Daphnia*, where offspring born from mothers that have been exposed to predatory stimuli grow larger defensive helmets (Agrawal et al. 1999). Similar processes also operate in plants, for example in *Campanulastrum americanum*, where offspring phenotypes are dependent on the maternal light environment, and those that experience a light environment that matches that of their mother have a 3.4 times larger

fitness in comparison to offspring that develop in different light conditions (Galloway and Etterson 2007). These examples show that in at least some cases, maternal effects facilitate offspring anticipation of environmental challenges.

In numerous other contexts, however, adaptive parental effects appear to be weak or absent (see Uller et al. 2013, for a meta-analysis), raising the question what limits the evolution of transgenerational plasticity. It is often suggested that the presence of parent–offspring conflict could be one of the factors responsible for the limited prevalence of adaptive parental effects (e.g., Wells 2003b; Müller et al. 2007; Uller 2008; Kilner and Hinde 2008; Tobler and Smith 2010; Uller et al. 2013), yet the consequences of parent–offspring conflict to the evolution of adaptive parental effects are still poorly understood. Parent–offspring conflict arises because offspring value their own survival more strongly than that of current or potential future siblings, while parents value all of their offspring equally (Trivers 1974; Parker and Macnair 1978; Kilner and Hinde 2008). Conflict between parents and offspring has seen substantial attention in the context of parental resource provisioning (e.g., Parker and Macnair 1978; Godfray 1995; Hinde et al. 2010; Kuijper and Johnstone 2012), yet it affects information exchange as well: in particular, much attention has been devoted to parental acquisition of information about offspring need or hunger, and to what extent parents can rely on offspring signals of condition (Godfray 1991; Godfray and Johnstone 2000; Royle et al. 2002; Wells 2003a). Other studies have considered whether mothers can skew information to manipulate offspring social behaviors (e.g., Pen and Taylor 2005; González-Forero and Gavrilets 2013; González-Forero 2015). Here, by contrast, we are concerned with acquisition of information about the external environment by offspring from their parents, but similar issues arise within each context of information exchange (Uller and Pen 2011; González-Forero 2014). When there is parent–offspring conflict over the optimal offspring phenotype, can offspring rely on maternal signals about the environment? Alternatively, might maternal effects provide a means by which mothers can manipulate offspring phenotypes and enforce their own optima on their young?

So far, how parent–offspring conflict affects the evolution of informative maternal effects has seen surprisingly little formal investigation. A single model by Uller and Pen (2011) has considered how parent–offspring conflict over dispersal affects the degree of information contained in maternal effects. Unless offspring are somehow constrained in their response to maternal signals, they find that parent–offspring conflict typically does not affect the evolution of informative maternal effects, so that at evolutionary equilibrium, offspring are able to rely on maternal signals to implement their own optimal strategy. This contrasts markedly with other signaling models that focus on information transfer from offspring to parents, which suggest that conflict leads to the breakdown of informative signaling, unless honesty is maintained by some form of signal cost (Godfray et al. 1991; Johnstone 1999; Godfray and Johnstone 2000). Consequently, this raises the question of whether informative signaling by mothers to offspring is indeed a general outcome of parent offspring conflict, as suggested by Uller and Pen (2011), or whether there are contexts in which conflict can lead to a breakdown of informative maternal signals instead.

To assess how parent–offspring conflict affects the evolution of maternal effects, we focus on a scenario of conflict over offspring local adaptation in a spatiotemporally varying environment (Leimar and McNamara 2015; English et al. 2015; Kuijper and Johnstone 2016). Fluctuating environments often favor parents that produce a mixture of offspring phenotypes, containing some offspring that are adapted and some offspring that are maladapted to the current state of the local environment (Starrfelt and Kokko 2012). Producing a mixture of offspring phenotypes ensures that at least some offspring are likely to survive, even if the local environment changes, thus preventing the extinction of the parental gene lineage (Ellner 1986; McNamara 1995; Leimar 2005). In contrast to their parents, however, individual offspring have a higher genetic interest in their own survival than in that of their siblings. Consequently, offspring favor a lower probability of developing a currently maladapted phenotype than do their parents, resulting in parent–offspring conflict over local adaptation.

We explore a situation in which offspring cannot assess the environment they will experience directly for themselves, but must rely on signals from their mother. A key ingredient of our model is that mothers can potentially "skew" the information they provide, by signaling in a misleading way. The question we then seek to answer is whether reliable maternal signaling is stable, allowing for the persistence of maternal effects, or whether it is vulnerable to disruption by maternal dishonesty.

The Model

We consider an "infinite island" model (Wright 1931; Rousset 2004; Lehmann and Rousset 2010) comprising a sexually hermaphroditic metapopulation that is distributed over an infinite number of patches, each of which contains n adult breeders. Generations are discrete and nonoverlapping, and in each generation, every breeder produces, as mother, a large number of offspring, each of which is sired by a random breeder. With probability ℓ, this sire is chosen from the same patch as the mother (including the possibility of self-fertilization), while with probability $1-\ell$ the sire is chosen from a random remote patch. For the sake of tractability, we assume that the population is haploid, where gametes are produced clonally and pair to form diploid zygotes, which immediately undergo meiosis to form a new generation of haploid offspring (individual-based simulations assuming diploid

inheritance and a finite number of patches give similar results, see Figs. S6– S8). Upon birth, a fraction $1 - d$ of newborn young remain on the natal patch, while the remaining fraction d disperse to a random patch in the metapopulation. After dispersal, offspring on a patch, both native and immigrant, compete for the n breeding vacancies created by the death of the previous generation. Those that fail to obtain a breeding vacancy die, and the life cycle then repeats. Below we provide a verbal summary of the model, while a more extensive description is given in Section S2 of the Online Supporting Information.

ENVIRONMENTAL VARIATION

Following previous models of maternal influences on offspring phenotype determination that do not consider parent-offspring conflict (e.g., Shea et al. 2011; English et al. 2015; Leimar and McNamara 2015; Kuijper and Johnstone 2016), we consider a spatiotemporally fluctuating environment in which each patch fluctuates between two environmental states, e_1 and e_2. In each generation, an e_i patch can change to an e_j patch with probability $\sigma_{i\to j}$ $(i \neq j)$ while it remains in environmental state e_i with probability $1 - \sigma_{i\to j}$. Patches fluctuate independently of one another, so that at any given time a proportion $p_1 = \sigma_{2\to1}/(\sigma_{1\to2} + \sigma_{2\to1})$ of patches is in environmental state e_1, while the remainder $p_2 \equiv 1 - p_1$ is in environmental state e_2.

PHENOTYPE DETERMINATION

Upon birth of an offspring, it can adopt one of two phenotypes, z_1 or z_2. Individuals are "locally adapted" and therefore experience a lower mortality rate when their phenotype z_i is identical to the environment e_i of their patch (Kawecki and Ebert 2004). Individuals are characterized by the genetically determined strategy f_i that reflects the probability that an offspring develops phenotype z_1 as opposed to phenotype z_2. Importantly, f_i may depend upon an offspring's natal environment e_i, so we consider the evolution of a strategy $\mathbf{f} = \{f_1, f_2\}$ that specifies phenotype determination probabilities for each of the two environments. Our model also accounts for the possibility that offspring of one phenotype are potentially more costly to the mother (i.e. they require more maternal resources) than offspring of the opposite phenotype (e.g., Trivers 1974; Ellner 1986; Kuijper and Pen 2014). Moreover, we allow such maternal production costs to vary dependent on the local environment e_i, so that the parameters β_i and γ_i reflect the maternal cost of producing a z_1 and z_2 offspring respectively when the local environment is in state e_i. Hence, the average investment E_i by a mother living in environment e_i per offspring is proportional to $f_i\beta_i + (1 - f_i)\gamma_i$. Following classical life-history models (Smith and Fretwell 1974; Parker and Macnair 1978), we assume that the total number of offspring produced is inversely proportional to the average investment per offspring. Consequently, the numbers of z_1 and z_2 offspring produced by a mother living in environment e_i are then given by f_i/E_i and $(1 - f_i)/E_i$, respectively. After phenotype determination, offspring either disperse or stay in the local patch, with dispersal occurring prior to environmental change. The survival probability of an offspring with phenotype z_j that ends up competing in a patch that is in environmental state e_j is given by ω_{ij}. Throughout, we assume that offspring with a phenotype that matches the local environment always survive, so that $\omega_{11} = \omega_{22} = 1$, while z_1 offspring in an e_2 environment survive with probability $\omega_{12} = 1 - c_2$ and z_2 offspring in an e_1 environment survive with probability $\omega_{21} = 1 - c_1$. All surviving offspring in a patch, both immigrant and philopatric, then compete for the n adult breeding positions that are locally available. The resulting fitness equations, which describe the number of successfully established offspring born from adults living in each environment are set out in Section S2.1 of the Online Supporting Information.

MAPPING THE BATTLEGROUND

The question now arises to what extent the evolutionary interests of parents and offspring diverge when it comes to the decision of developing phenotype z_1 versus z_2. To resolve this issue, we compare the evolutionarily stable values of f_1 and f_2 under maternal and under offspring control (the divergence between these outcomes defining the "battleground" within which parent–offspring conflict will be played out, Godfray 1995). To determine the equilibrium probabilities of producing a z_1 phenotype under either maternal or offspring control, we adopt an adaptive dynamics approach (Geritz et al. 1998; Rousset 2004; Dercole and Rinaldi 2008). This assumes that evolution proceeds by the successive substitution of mutations of small effect, with a clear separation of time scales between demographic and evolutionary processes (Otto and Day 2007). We use a direct fitness (also called neighbor-modulated fitness) approach (Taylor and Frank 1996; Taylor et al. 2007) to derive the selection gradient $\mathcal{F}_i$ that determines the evolutionary change in the probability f_i of producing a z_1 offspring in environment e_i (see eq. [S5]). By numerically iterating the selection gradients until they vanish, we are able to solve numerically for the equilibrium probabilities f_1^*, f_2^* of producing a z_1 phenotype in each of the two environments. To provide the clearest possible picture of the battleground and its consequences, we focus on a scenario where there is strong competition among kin, as this is known to enhance parent–offspring conflict (e.g., Taylor 1988; Kuijper and Johnstone 2012). We do so by focusing on a scenario where there is a single hermaphrodite parent per patch $(n = 1)$ with a rate of nonlocal mating of $1 - \ell = 0.5$, as this results in substantial divergence of parental and offspring optima across all scenarios. However, we have also explored other parameters (e.g., $n = 2$, $n = 5$, $\ell = 1.0$, $d = 0.8$, and combinations thereof). While we find that the divergence between parental and offspring optima is typically smaller, coevolutionary outcomes (in

terms of how conflict affects information content and who wins the conflict) are qualitatively similar to the results depicted here.

RESOLVING THE CONFLICT

If the interests of mothers and offspring diverge, how then might maternal-offspring conflict be resolved? If offspring must rely on mothers for information about the state of the local environment, could this enable mothers to manipulate the behavior of their young in each of the two contexts considered? To evaluate this possibility, we suppose that mothers can assess the state of the local environment, while offspring cannot (see also Uller and Pen 2011). Mothers may choose to give or to withhold a signal from each of their young, with probabilities of giving the signal dependent on the state of the local environment. Offspring may then choose to develop phenotype z_1 or z_2, with probabilities dependent on whether or not they have received a signal from their mother.

The maternal signaling strategy $\mathbf{s} = (s_1, s_2)$ thus specifies the probabilities of giving (rather than withholding) the signal in each type of patch, while the offspring phenotype determination strategy $\mathbf{q} = (q_S,\ q_{NS})$ specifies the probabilities of developing a z_1 phenotype when a signal is or is not received. It is the combination of these two strategies that determines the fraction of young f_i that develop as z_1 in each environment e_i:

$$f_i\ (s_i, q_S, q_{NS}) = s_i q_S + (1 - s_i) q_{NS}, \tag{1}$$

so that with probability s_i a mother living in environment e_i provides her offspring with a signal, who will therefore develop as a z_1 offspring with probability q_S (and as a z_2 offspring with probability $1 - q_S$). By contrast, with probability $1 - s_i$, the mother withholds the signal, in which case offspring develops as a z_1 or z_2 offspring with probabilities q_{NS} and $1 - q_{NS}$, respectively. Associated fitness expressions for the maternal signaling probabilities and offspring phenotype determination strategies are given in equations (S17–S20) in the Online Supporting Information. We again assume that evolution proceeds by the successive substitution of mutations of small effect, with a clear separation of time scales between demographic and evolutionary processes (Otto and Day 2007). This allows us to use a direct fitness approach to derive the selection gradients $\mathcal{S}_i$ and $\mathcal{Q}_j$ that determine the rates of evolutionary change in the probability s_i of providing offspring a signal in each environment and the probability $q_j \in \{q_S, q_{NS}\}$ of producing a z_1 offspring in the presence or absence of a signal (see eqs. [S21, S22]).

To solve the conflict resolution model, we seek to identify equilibrium strategy pairs for which all selection gradients (for both strategies) are simultaneously equal to zero. To do so, we choose initial conditions such that the signal is highly informative (e.g., we might choose $s_1 = 0.9$ and $s_2 = 0.1$) and offspring highly responsive (e.g., $q_S = 0.9$ and $q_{NS} = 0.1$), and iteratively update the signaling and phenotype determination probabilities by adding to each the value of the relevant selection gradient (given the current strategies), bounding the updated values between 0 and 1. This procedure is repeated until all strategies converge to stable values. The solutions obtained in this way are robust to changes in the precise starting conditions chosen, and convergence stable by construction. Note, however, that two mirror-image signaling equilibria are possible in any particular case— one in which the signal is given more often in environment e_1 and withheld more often in environment e_2, and one in which the signal is given more often in environment e_2 and withheld more often in environment e_1. These provide offspring with equal information, and thus have identical consequences in terms of the phenotype determination rates out of each patch type. For ease of interpretation, however, we consistently choose starting conditions in which the signal is given more often in environment e_1. Individual-based simulations, which assume a continuous distribution of mutations and no necessary separation of timescales, yield results that are quantitatively very similar to analytical model (see Figs. S6– S8).

Results

THE BATTLEGROUND

Figure 1 illustrates the ways in which the interests of mothers and offspring diverge. The graphs show the stable fraction of z_1 offspring produced in environment e_1 (blue) and in environment e_2 (red), under maternal control (dotted lines) versus under offspring control (solid lines), as a function of c_2, the cost of maladaptation in environment e_2 (while holding c_1, the cost of maladaptation in environment e_1, constant at 0.83). In general, both mothers and offspring favor higher proportions of z_1 offspring when the cost of maladaptation in environment e_2 is low (at the left-hand side of each graph), and lower proportions of z_1 offspring when the cost of maladaptation in environment e_2 is high (at the right-hand side of each graph). However, stable outcomes under maternal versus offspring control rarely agree precisely.

The three panels of the figure show results for three different sets of parameter values, which we have chosen to illustrate three possible kinds of "disagreement" between mother and young (see Fig. S1 for a more extensive overview of model results).

Scenario 1 (panel A): offspring favor production of more of the locally adapted phenotype in each environment (i.e., more of phenotype z_1 in environment e_1, and more of phenotype z_2 in environment e_2); in terms of the graph, the red and blue solid lines for equilibria in the case of offspring control lie "outside" the corresponding dotted lines for equilibria in the case of maternal control. In this scenario, z_1 and z_2 offspring are equally costly to produce. Under these circumstances, mothers do best (in either environment) to hedge their bets by producing a certain fraction of

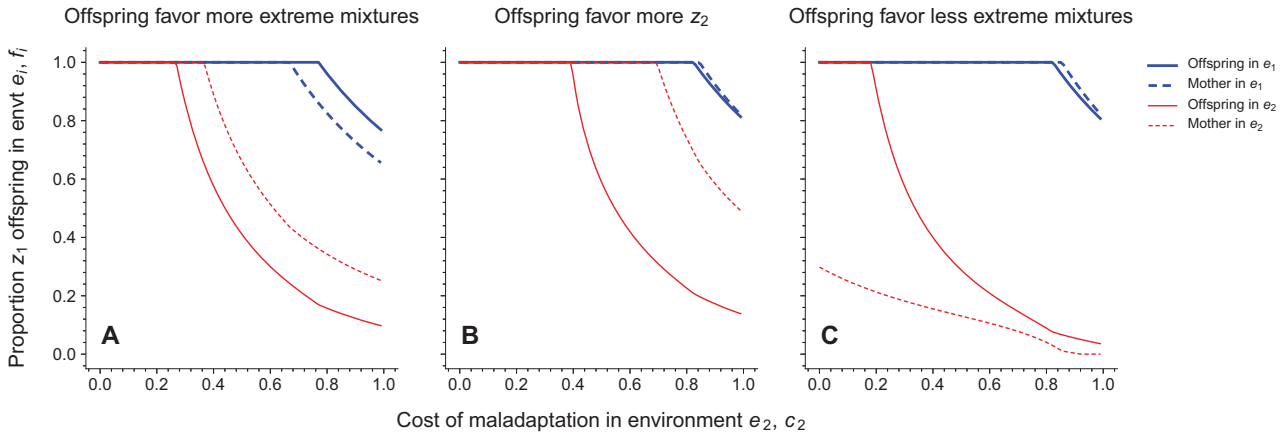

Figure 1. Stable probabilities of producing a phenotype z_1 offspring in environments e_1 (blue lines) and e_2 (red lines), respectively, plotted against the cost of maladaptation c_2 in environment e_2. (A) both offspring phenotypes are equally costly to produce to mothers ($\beta_1 = \beta_2 = \gamma_1 = \gamma_2 = 1$). Consequently, mothers (dashed lines) favor more even mixtures of offspring phenotypes. By contrast, offspring favor more extreme mixtures that are biased toward the phenotype with the highest survival in the local environment (i.e., offspring favor more z_2 in environment e_2 and more z_1 in environment e_1). (B) When phenotype z_2 is more costly to produce in both environments ($\beta_1 = \beta_2 = 1$, $\gamma_1 = \gamma_2 = 2$), the probability of producing z_2 offspring is reduced. However, as offspring are more related to themselves than to their mothers, offspring favor a greater probability of producing more costly z_2 offspring in both environments. (C) Maternal production costs are environment dependent, so z_2 young are more costly (less costly) to produce than z_1 young in environment e_1 (in environment e_2); ($\beta_1 = 1, \beta_2 = 2, \gamma_1 = 2, \gamma_2 = 1$). Consequently, mothers favor more extreme mixtures of offspring phenotypes that are biased toward the phenotype that is cheaper to produce in each environment. By contrast, offspring favor a larger probability of developing as the more costly phenotype, leading them to favor more even mixtures of offspring phenotypes. Parameters: $d = 0.1$, $\ell = 0.5$, $\sigma_{12} = 0.2$, $\sigma_{21} = 0.25$, $n = 1$, $c_1 = 0.83$.

young with a currently (locally) maladapted phenotype, to ensure survival of at least some of their brood in case the environment changes. Since offspring, by contrast, have a greater evolutionary interest in their own survival than in that of the brood as a whole, they favor a higher probability of developing the currently well-adapted phenotype.

Scenario 2 (panel B): Offspring favor production of more of phenotype z_2 across both environments; in terms of the graph, the red and blue solid lines for equilibria in the case of offspring control lie above the corresponding dotted lines for equilibria in the case of maternal control. In this case, z_2 offspring are twice as costly for mothers to produce as are z_1 offspring. Under these circumstances, mothers favor mixtures of offspring phenotypes that are more biased toward the cheaper z_1 phenotype across both environments, because producing a larger fraction of costly young reduces their overall fecundity. By comparison, offspring are less concerned with maternal fecundity relative to their own survival, and so favor mixtures of phenotypes that are more biased toward the expensive z_2 phenotype, across both environments.

Scenario 3 (panel C): Offspring favor production of more of the locally maladapted phenotype in each environment (i.e., more of phenotype z_2 in environment e_1, and more of phenotype z_1 in environment e_2); in terms of the graph, the red and blue solid lines for equilibria in the case of offspring control lie "inside" the corresponding dotted lines for equilibria in the case of maternal control. In this case, maternal costs of producing one phenotype versus the other are assumed to depend on the local environment: specifically, we assume that a z_2 young is twice as costly to produce as a z_1 young in environment e_1, while z_1 young are twice as costly to produce than z_2 young in environment e_2. In this case, mothers favor more extreme mixtures that are biased toward the the locally adapted phenotype that is the cheapest to produce in that particular environment, while offspring favor less extreme mixtures that feature more of the locally costly phenotype.

We have chosen parameter values to highlight the different kinds of conflict that can arise between mothers and young, because the nature of the "disagreement" turns out to affect the resolution of the conflict, as detailed below.

RESOLUTION OF THE CONFLICT

How is parent–offspring conflict resolved when offspring control the determination of their phenotype, but must rely on maternal signals about the state of the local environment? We can categorize outcomes of the model according to the extent of information supplied by mothers to their young - offspring may obtain (i) full information about the environment (because the presence or absence of the maternal signal is perfectly correlated with the state of the environment), (ii) partial information (because the signal is given more commonly in one environment than in the other,

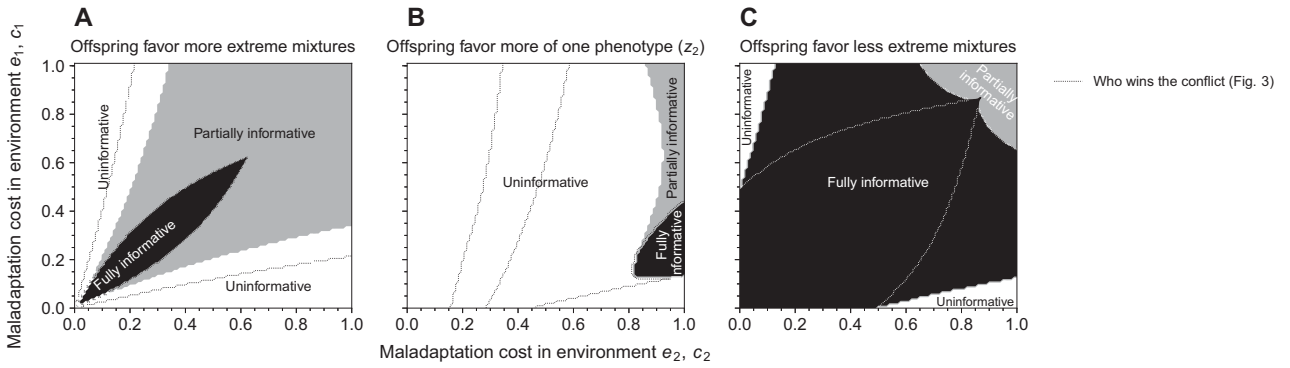

Figure 2. **Phenotype determination when offspring rely on the maternal signal: the information content of the maternal signal $s = (s_1, s_2)$ for the three different scenarios of conflict considered in Figure 1. (A) Offspring phenotypes are equally costly to produce to mothers. For a wide range of costs of maladaptation, mothers evolve signals that are partially informative to offspring, although other outcomes also occur. (B) When the z_2 phenotype is more costly to produce for mothers in both environments, maternal signals always evolve to be uninformative when conflict occurs. (C) When the z_1 and z_2 phenotypes are more costly to produce in the respective environments e_2 and e_1, maternal signals typically evolve to be fully informative, apart from a narrow boundary in which signals are only partially informative. Dotted lines delineate who wins the conflict (see Fig. 3). The information content H is calculated as the absolute difference between the two maternal signals, $H = |s_1 - s_2|$. See Figure S2 for the corresponding equilibrium probabilities of producing offspring with phenotype z_1 when offspring rely on a maternal signal. In addition, Figure S3 plots outcomes for other environmental configurations. Parameters: $d = 0.1$, $\ell = 0.5$, $\sigma_{12} = 0.15$, $\sigma_{21} = 0.15$, $n = 1$.**

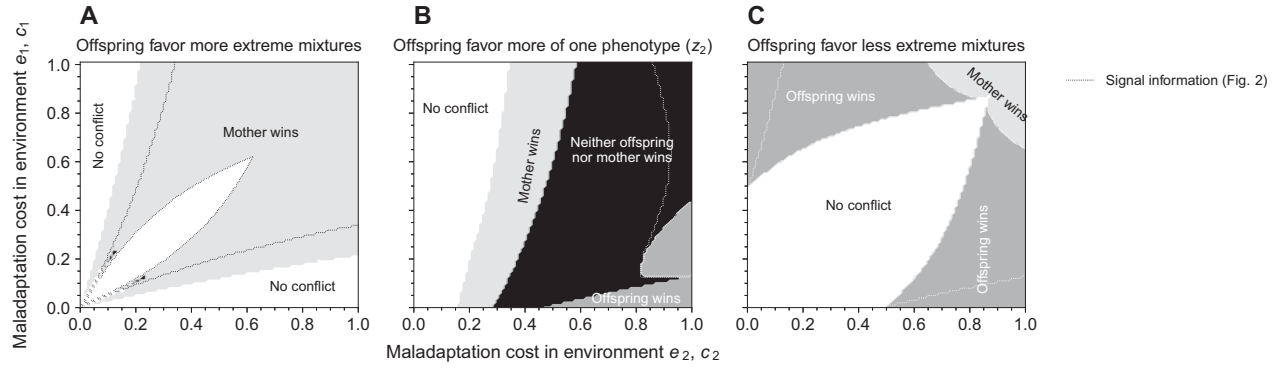

Figure 3. **Phenotype determination when offspring rely on the maternal signal: who wins the conflict? (A) When offspring favor more extreme mixtures of phenotypes than mothers, mothers can be said to win the conflict by restricting the information content of the maternal signal. (B) When offspring favor mixtures that are more biased toward one phenotype (z_2) relative to their mothers, the conflict is either won by offspring, mothers or neither of them, dependent on the relative strength of the costs of maladaptation in each environment. (C) When offspring favor mixtures that are less extreme relative to what is favored by their mothers, offspring win the conflict, as a fully informative maternal signal never results in more extreme mixtures than what is favored by offspring. Dotted lines depict whether signals are uninformative, partially informative or fully informative (see Fig. 2). In addition, Figure S4 plots outcomes for other environmental configurations. Parameters: $d = 0.1$, $\ell = 0.5$, $\sigma_{12} = 0.15$, $\sigma_{21} = 0.15$, $n = 1$.**

but the correlation is imperfect) or (iii) no information (because the presence or absence of the signal is uncorrelated with the environment).

Alternatively, taking into account both the probabilities of the signal being given or withheld, and the response of offspring in each case, we can categories outcomes according to the degree to which the realized probabilities of producing each phenotype match the values favored by mothers versus young - (i) parents may win (i.e., the outcome matches what evolves under maternal control), (ii) neither "side" may win (i.e., the outcome diverges from what evolves under either maternal or offspring control), or (iii) offspring may win (i.e., the outcome matches what evolves under offspring control). Figure 2 shows the regions of parameter space in which the model predicts different levels of information transfer, while Figure 3 shows the regions in which mothers or offspring (or neither) are predicted to win (with equivalent results for additional regions of parameter space shown in Figs. S3 and S4).

As detailed below, comparison of Figures 2 and 3 with Figure 1 reveals that there is not necessarily a strict relationship

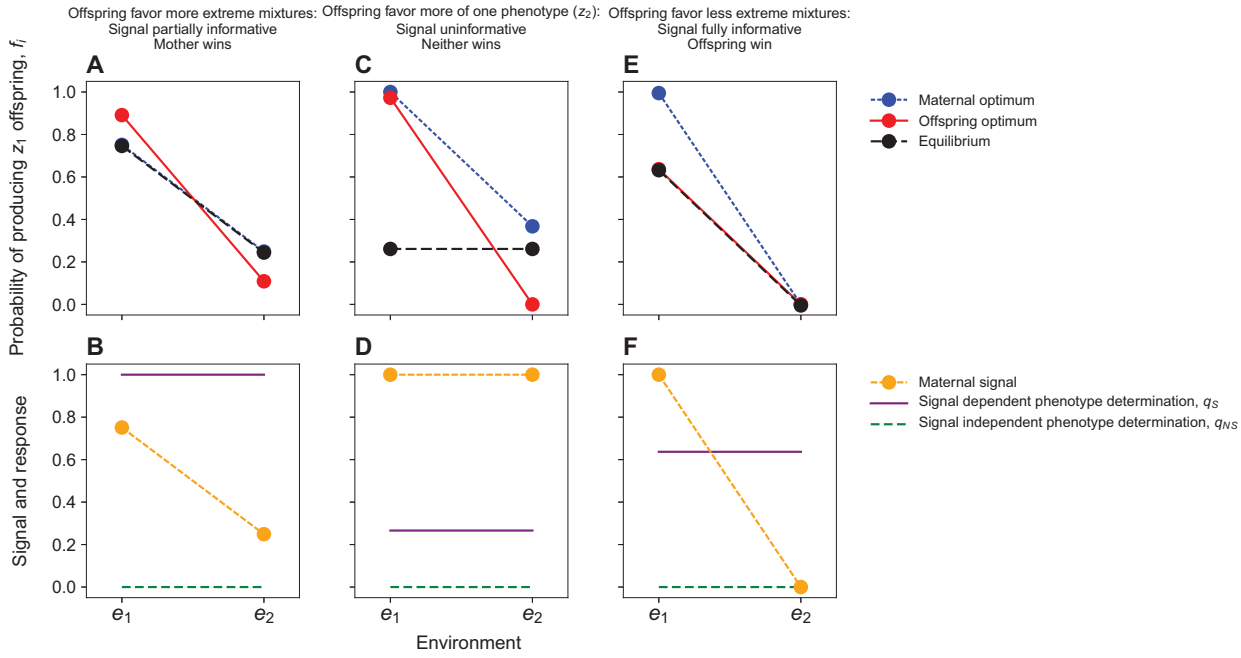

Figure 4. **Examples of phenotype determination strategies (top row) and resulting signaling strategies (bottom row). (A, B) When offspring favor more extreme mixtures of phenotypes than mothers, mothers evolve only partially informative signals (B). As offspring only receive a limited amount of environmental information, offspring produce less extreme phenotypic mixtures, and mothers win the conflict (A). (C, D) When offspring favor phenotypic mixtures that are more biased toward one phenotype (z_2), uninformative maternal signals commonly evolve (D), so that neither parents nor offspring win the conflict (C). (E, F) When offspring favor less extreme mixtures of phenotypes than mothers, mothers evolve fully informative signals (F). As a result, offspring obtain complete environmental information, resulting in offspring winning the conflict (C). Parameters: $d = 0.1$, $\ell = 0.5$, $\sigma_{12} = \sigma_{21} = 0.15$, $n = 1$. Specific parameters for the different panels: A, B: $c_1 = c_2 = 0.95$, $\beta_1 = \beta_2 = \gamma_1 = \gamma_2 = 1$; C, D: $c_1 = 0.5$, $c_2 = 0.8$, $\beta_1 = \beta_2 = 1$, $\gamma_1 = \gamma_2 = 2$; E, F: $c_1 = 0.2$, $c_2 = 0.8$, $\beta_1 = \gamma_2 = 1$, $\beta_2 = \gamma_1 = 2$. The scenario in panels C, D where offspring favor phenotypic mixtures that are more biased toward one phenotype (z_2) is further highlighted in Figure S5.**

between the nature of the parent/offspring battleground and the outcome (in terms of either information conveyed or who wins the battle). At the same time, however, there is a strong correlation, such that each of the three battleground scenarios we list above is typically associated with a different kind of outcome.

Result 1: When offspring favor more extreme mixtures than their mothers, mothers typically win the conflict by providing partial information

When offspring favor more extreme mixtures of phenotypes relative to their mothers (as in Fig. 1A), maternal signals often evolve to be partially informative to offspring, particularly when survival costs of a maladapted offspring (c_1, c_2) are large in both environments (Fig. 2A, top right corner). In this case, offspring are selected to rely on maternal information, as the alternative results in substantial costs due to local maladaptation. However, by limiting the amount of information about the local environment, mothers force offspring to increase their level of bet-hedging, thus resulting in a less extreme mixture of offspring phenotypes that coincides with the maternal optimum (see Fig. 3A). An example of such a partially informative signaling strategy is given in Figures 4A, B (see Fig. S6 for a corresponding individual-based simulation).

Note, however, that coevolution between maternal signals and offspring responsiveness can also lead to alternative outcomes: when the cost of maladaptation is large in one environment, but small in the other, maternal signals evolve to become uninformative (white regions in Fig. 2A), as mothers favor the exclusive production of a single offspring phenotype (the one that matches the most severe environment) across the two environments. Conversely, when costs of maladaptation are modest and of similar magnitude in both environments, parental and offspring optima align, leading parents to evolve signals that are fully informative to offspring (black region in Fig. 2A).

Result 2: When offspring favor more of one phenotype, then typically neither side wins, and signaling often breaks down

As described above, when one phenotype is more costly to produce (in terms of maternal resources) than the other, offspring favor mixtures in both environments that are more biased toward the more expensive phenotype (here z_2) than do mothers (see

the battleground in Fig. 1B). By far the commonest outcome for this type of battleground is that signaling breaks down (white areas in Fig. 2B), thus resulting in unconditional offspring phenotype determination strategies. Who wins the conflict now starts to depend on the relative costs of maladaptation (Fig. 3B): when survival costs of maladaptation are high in environment e_1, yet very low in environment e_2 (white regions in Fig. 3B), both parents and offspring favor the production of a single phenotype (z_1; which matches the most severe environment) across both environments, so conflict is absent. When costs of maladaptation in environment e_2 are slightly larger, however, offspring born in environment e_2 favor the production of costly z_2 offspring, while mothers still favor the production of cheaper z_1 offspring in both environments. However, in the presence of an uninformative signal, offspring are forced to play an unconditional strategy that results in the exclusive production of z_1 offspring in both environments, so that mothers can be said to win the conflict (light gray area in Fig. 3B).

For higher costs of maladaptation in environment e_2 (top middle of Figure 3B), mothers now favor to produce some z_2 offspring in environment e_2. However, as offspring favor a much higher probabilities of z_2 development in environment e_2, mothers are selected to withhold any information to offspring (see Fig 4C, D for a detailed example). However, offspring now favor the production of a mixture of both z_1 and z_2 offspring in the absence of any maternal information, so that the resolution is one in which neither parent nor offspring wins the conflict (black region in Fig. 3B). Although neither parents nor offspring win the conflict, we find that the resulting phenotype determination strategies lie slightly closer to the offspring rather than the maternal optima when costs of maladaptation are modest in environment e_2 and small in environment e_1 (bottom of black region). By contrast, when costs of maladaptation in environment e_1 become larger (top of black region), the resulting phenotype determination strategies lie closer to the maternal rather than the offspring optima (e.g., see Fig. 4C).

Finally, for even higher costs of maladaptation in environment e_2 (right part in Fig. 2B), mothers now favor to provide some information to offspring, to prevent an unconditional offspring strategy where a large number of costly z_2 offspring are produced regardless of the environment. (see Fig. S5A, B for a detailed example). However, as offspring favor a larger proportion of z_2 offspring in environment e_2 than mothers do, mothers only provide a partially informative signal to offspring (dark gray area in Fig. 2B). The resulting uncertainty leads to less extreme proportion of z_2 offspring in environment e_2, but also leads to the production of some z_2 offspring in environment e_1. Consequently, again neither parents or offspring can be said to win the conflict (see Fig. S5A).

Result 3: When offspring favor less extreme mixtures than their mothers, offspring typically win the conflict, with mothers providing full information

When phenotype z_2 is more costly to produce in environment e_1, while phenotype z_1 is more costly to produce in environment e_2, mothers favor mixtures that are more extreme than offspring do (see the corresponding battleground in Fig. 1C). Regarding the resolution of the conflict, Figure 2C shows that maternal signals typically evolve to be fully informative. In addition, Figure 3C shows that, for this configuration of maternal production costs, there is a substantial region where conflict is absent. However, when conflict occurs, offspring typically win the conflict as a result of these fully informative signals.

A more detailed example is shown in Figure 4E, F: to avoid the production of offspring that are more costly in terms of maternal resources, mothers favor extreme mixtures consisting only of z_1 offspring in environment e_1 and only of z_2 offspring in environment e_2 (blue dotted line in Fig. 4E). Offspring, however, favor a less extreme mixture of phenotypes (red solid line). Mothers are then selected to provide offspring with the maximum amount of information, as this yields mixtures of phenotypes that are closest to what is favored by the mother. By contrast, would mothers reduce the information content of the maternal signal, they would only select offspring to produce even less extreme mixtures that are even further away from the maternal optima. Hence, provided with complete environmental information, offspring can attain their respective optima in each environment (black dotted and red lines overlap in Fig. 4E).

Next to the evolution of fully informative signals, Figure 2C also highlights two alternative outcomes that occur in much smaller regions of the parameter space: first, when costs of maladaptation are extremely asymmetric across environments (top left and bottom right corners of Fig. 2C), offspring favor to exclusively produce the offspring phenotype that matches the most severe environment, and hence do not require any maternal information. Finally, when costs of maladaptation are high across both environments (top right corner of Fig. 2C), maternal signals evolve to be partially informative and mothers now win the conflict. Due to severe offspring survival selection in this part of the parameter space, mothers are selected to hedge their bets by producing a more even mixture of offspring phenotypes, even when this implies that part of her offspring are costly to produce in terms of maternal resources. As a consequence, offspring now favor a mixture that is more biased toward the currently adapted phenotype relative to the mixture favored by mothers, so that the battleground in Figure 1A applies, resulting in coevolutionary outcomes as observed in Figure 2A.

Discussion

Our main conclusion is that parent–offspring conflict can have a significant impact on the evolution of informative maternal effects, even when offspring are unconstrained in their responses. The key feature of our model that leads to this outcome is that parents are allowed to adopt an imperfectly informative signaling strategy, and to "skew" offspring responses toward their preferred outcome by independently adjusting the probabilities with which they give or withhold signals in each environment. When mothers can potentially manipulate offspring in this way, we find that parent–offspring conflict often leads to a partial or even a complete breakdown in information transfer at equilibrium (just as it can do in models of signaling of need by offspring to their parents, Johnstone and Godfray 2002). Consider, for instance, the case in which parents favor a higher proportion of a cheaper phenotype among their young, compared to that favored by their offspring, and in which they do so regardless of the local environment. Under these conditions, it is hard for informative maternal signals to persist. If offspring take advantage of this information by responding to such a signal, an individual mother can always "push" her young closer toward her own optimum by misrepresenting the state of the environment, and signaling in a way typical of local conditions that elicit a higher proportion of the cheaper phenotype. Consequently, we conclude that parent–offspring conflict may provide a powerful explanation for the apparent weakness of transgenerational plasticity in nature (for reviews see Uller et al. 2013; Heard and Martienssen 2014).

Our finding that parent–offspring conflict often leads to the breakdown of informative maternal effects contrasts with the pioneering study by Uller and Pen (2011), which is the first to model the evolution of maternal effects when parents and offspring are in conflict over dispersal. In contrast to our model, Uller and Pen (2011) find that offspring typically evolve to be highly sensitive to maternal information about the state of the environment, regardless of any discrepancy between maternal and offspring optima. Here, we highlight some of the assumptions in Uller and Pen (2011) that could potentially explain the difference in outcomes between both studies: first, their model assumes that offspring are provided with a signal m_i that is tied to a particular patch type e_i. Consequently, even the slightest divergence between maternal signals in each environment (i.e., $m_i \neq m_j$) provides offspring with perfect information about the environment. In other words, mothers are only able to withhold information to offspring when they are able to hold the signal m_i exactly equal to m_j, which would require considerable canalization in the face of mutation and drift in either signal. The alternative option, where mothers withhold information by simply evolving no signal at all ($m_i = m_j = 0$) is not possible in the model by Uller and Pen (2011), because of their assumption that any reduction of the maternal signal always reduces offspring dispersal (e.g., see their eq. [9]). Lower values of the maternal signal that reduce dispersal will always be selected against, because mothers always favor higher rates of dispersal relative to offspring (e.g., see Motro 1983; Taylor 1988). Consequently, nonzero and informative maternal signals will evolve by definition in the model by Uller and Pen (2011).

In a supplementary model, Uller and Pen (2011) also analyze the evolution of maternal assessment errors, where making an error in environment e_i implies that all her offspring are provided with signal m_j rather than signal m_i. However, they find that these maternal errors do not evolve, in contrast to our model where mothers often produce signals with a reduced information content. One reason for this is that Uller and Pen (2011) assume that a maternal error affects the whole brood: in other words, even when a mother only makes an error with a slight probability, once she does so, all of her young receive the wrong environmental information, resulting in costly maladaptation of her whole brood (brood-level errors). By contrast, the current model assumes that a mother signals to each individual offspring independently, so that a slight maternal error implies that only a subset of a her young will receive the wrong information (individual-level errors).

Next, the error in the model by Uller and Pen (2011) is constrained to be identical (and hence symmetrical) across both environments. However, in case of parent–offspring conflict over dispersal, such symmetric errors will not evolve. This is because manipulating offspring to disperse more from environment e_i (by providing young with an erroneous signal associated to the high-dispersal environment e_j) has the disadvantage that offspring will be similarly manipulated to have a lower dispersal probability from the other environment e_j (as those young will receive an erroneous signal associated to the low-dispersal environment e_i). Because mothers typically favor higher rates of dispersal than offspring across both environments (e.g., see Motro 1983; Taylor 1988), symmetric errors will thus not be favored. Only when parents can independently adjust the probability of a signal being given in each environment (i.e., asymmetric errors), is there a possibility for parents to skew offspring responses in their own favor by misrepresenting the environment in a biased manner. Indeed, we find that such asymmetric, individual-level errors rapidly evolve in the simulation model by Uller and Pen (2011) (Johnstone and Kuijper, unpubl. ms.). Note, however, that symmetric errors may still evolve in scenarios of parent–offspring conflict other than dispersal: for example, in a scenario where mothers favor more even mixtures of phenotypes (as in Fig. 4A, B) symmetric individual-level errors evolve (results not shown).

The comparison between the model by Uller and Pen (2011) and ours thus highlights a number of constraints on maternal manipulation that would prevent the breakdown of maternal effects: first, when offspring have some means of enforcing honesty of maternal signals, for example by evolving sensitivity to only

those signals that are costly to produce (Grafen 1990; Johnstone and Grafen 1992), mothers can be constrained from manipulating their young (Müller et al. 2007; González-Forero and Gavrilets 2013). In addition, when a mother is unable to signal to each of her young independently, the scope for maternal manipulation is also likely to be reduced. However, the generality of this constraint remains to be evaluated: for example, some studies find that there is substantial variation in DNA methylation among gametes from the same human parent (e.g., Jenkins et al. 2015; Yu et al. 2017), showing that individual-level signaling to young is certainly possible. Also, studies on avian hormones show that mothers are able to adjust hormone levels on a per-egg basis (e.g., Eising and Groothuis 2003) although between-clutch variation in hormone levels is typically larger than within-clutch variation (Groothuis et al. 2005; Postma et al. 2014). For other forms of mother-to-offspring signaling (e.g., acoustics: Mariette and Buchanan 2016), it might be more difficult for mothers to confine signals to individual offspring. Finally, mothers are also prevented from manipulating offspring (at least in contexts such as dispersal) when they cannot misrepresent the environment in a biased manner (e.g., when mothers are unable to signal with more error in one environment than another). Consequently, while the scope for maternal manipulation should always be considered (as in any signaling model, Dawkins and Krebs 1978; Laidre and Johnstone 2013), more should be done to assess how signals vary among individual offspring and what mechanisms mothers can use to misrepresent the environment.

Another key conclusion of our model is that when a reduction in maternal information transfer occurs, it does not necessarily imply that either mothers (or offspring) win the conflict. Rather, the outcome of the conflict typically depends on the nature of the disagreement between mothers and young (see Fig. 1), which depends on the specific trait that is studied. We suggest that scenarios in which mothers favor a more even mixture of phenotypes than do offspring (see Fig. 1A) are more likely to result in partially informative signals and mothers winning the conflict (see Fig. 3A). This type of outcome is particularly likely when alternative offspring phenotypes impose roughly similar costs on their mothers. One possible example is when individuals bet-hedge defenses against multiple stressors, as they do when resistance to one strain of parasite trades off against resistance to another strain (strain-specific immunity: Little et al. 2003; Schmid-Hempel 2005). While resistance in such contexts is often studied in the context of heterozygosity (e.g., Penn et al. 2002), an accumulating number of studies have shown that parasite resistance is, in part, influenced by transgenerational effects (Little et al. 2003; Boulinier and Staszewski 2008; Roth et al. 2009; Rechavi 2014; Pigeault et al. 2016). Our model predicts that parents would be selectively favored to produce more even mixtures of offspring resistant to one parasite strain versus another, while offspring themselves favor resistance against the parasite that is commonest in current local environment. In contexts like these, we would expect that mothers only provide their offspring with limited amounts of information about local parasite prevalence (leading to limited amounts of transgenerational plasticity—Uller 2008; Holeski et al. 2012), resulting in mothers winning the conflict.

For those traits for which offspring always favor overproduction of the costliest phenotype relative to mothers (see Fig. 1B), it is more difficult to predict who wins the conflict: dependent on the parameters involved, either the offspring, the mother, or neither wins the conflict (Fig. 3B). More important, however, is our finding that maternal information transfer can completely break down in this scenario, resulting in an absence of transgenerational plasticity (Fig. 2B), which is particularly likely to occur when costs of maladaptation are modest. We believe that the battleground depicted in Figure 1B applies to numerous traits that have been previously studied in the context of parent–offspring conflict. For example, when the trait in question is offspring size (Smith and Fretwell 1974), offspring will always favor a larger size than mothers themselves (Parker and Macnair 1978; Einum and Fleming 2000; Parker et al. 2002; Kuijper and Johnstone 2012). Similarly, when the trait in question is germination or diapause, offspring favor earlier germination than do their mothers because this enhances their probability of survival, while mothers favor later germination because this reduces competition with siblings (Ellner 1986). Finally, in the context of sex allocation, mothers favor overproduction of the cheaper sex (Trivers 1974; Kuijper and Pen 2014), or the sex that is least affected by local competition (Werren et al. 2002; Pen 2006; Wild and West 2009).

For those traits for which offspring favor less extreme mixtures relative to their mothers (see Fig. 1C), we predict that it is nearly always offspring who win the conflict (Fig. 3C). More importantly, we predict that maternal signals are often fully informative in such scenarios. Essentially, this scenario would apply when young with a maladapted phenotype would not only have a lower survival in the local environment, but also demand more resources from their mother relative to young with locally adapted phenotypes. While phenotype-dependent survival is a well-studied aspect of local adaptation (Kawecki and Ebert 2004; Savolainen et al. 2013), we are not aware of studies that demonstrate that locally maladapted offspring are also more costly to produce in terms of maternal resources. To encourage more studies to investigate the maternal resource costs of local adaptation, here we highlight a putative scenario of foraging specialization that could result in the battleground of Figure 3C: in some taxa, offspring decide early in life to specialize either on one local resource versus another (Bolnick et al. 2003). Some offspring may then specialize on a local resource that is currently abundant, while others may decide to specialize on a local resource that is

currently rare, but which may be abundant elsewhere or in a future generation. Offspring specialized on the locally rare resource may then have a low survival, and importantly, may also be more reliant on costly foraging and provisioning by their mothers to partially compensate a maladapted young's shortfall in resources. In this case, we would predict that mothers are selectively favored to provide full information to their young about the local environment, to limit the number of offspring who specialize on the rare resource, and who may require more costly maternal care relative to other young. We therefore urge future studies to assess the relevance of this scenario or other ways in which mothers pay increased costs to nurture locally maladapted young.

Summing up, we make two main, testable predictions. First, since parent-offspring conflict will often partially or completely destabilize maternal signaling, we predict that informative maternal effects are more likely to evolve, and to exert stronger effects, where conflict between parent and offspring is less pronounced. In other words, informative maternal effects should be strongest in contexts of female monogamy or when females reproduce asexually. Such a prediction could, for example be tested among closely related species with different mating systems, as is the case for the nematode genus *Caenorhabditis* (Fierst et al. 2015; Teotónio et al. 2017). Second, given that the impact of parent–offspring conflict depends upon the nature of the disagreement between parent and offspring, we predict that at least partially informative maternal effects are most likely to evolve or persist (even in the face of parent–offspring conflict) when different phenotypes impose similar costs to mothers (e.g., bet-hedging against different strains of parasites), we would expect partially informative signals to evolve. By contrast, breakdown of maternal signaling is a more likely outcome for traits in which one offspring phenotype is more costly to mothers than other offspring phenotypes (e.g., dispersal, sex allocation, germination), particularly when the costs of local maladaptation are modest.

AUTHOR CONTRIBUTIONS

BK and RAJ developed the model and wrote the paper.

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Supporting Information

Additional Supporting Information may be found in the online version of this article at the publisher's website:

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Figure S1: Stable probabilities of producing a phenotype z_1 offspring in environments e_1 (first column) and e_2 (second column) respectively, plotted against the cost of maladaptation in each environment for comparable parameter values as in Figure 1.

Figure S2: Phenotype determination when offspring rely on the maternal signal: the equilibrium probabilities of producing offspring with phenotype z_1 in environment e_1 (panels A, C, E) and e_2 (panels B, D, F) respectively.

Figure S3: Phenotype determination when offspring rely on the maternal signal: the information content of the maternal signal $\mathbf{s} = (s_1, s_2)$ for various regimes of environmental change.

Figure S4: Who wins the conflict for the regimes of environmental change depicted in Figure S3.

Figure S5: Additional examples of phenotype determination strategies (top row) and signaling strategies (bottom row) when offspring favor more of one phenotype (z_2) than mothers (see also Figure 4 C, D) in the main text.

Figure S6: The evolution towards a partially informative equilibrium where phenotype determination diverges across the two environments: individual-based simulations.

Figure S7: Evolution towards an uninformative equilibrium where phenotype determination is identical across both environments: individual-based simulations.

Figure S8: Evolution towards a fully informative equilibrium where phenotype determination is strongly environment-dependent: individual-based simulations.

Supplementary Model Description: Derivation of the analytical model of parent-offspring conflict.