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E-Article

Maternal Effects in a Wild Songbird Are Environmentally Plastic but Only Marginally Alter the Rate of Adaptation

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abstract: Despite ample evidence for the presence of maternal effects (MEs) in a variety of traits and strong theoretical indications for their evolutionary consequences, empirical evidence to what extent MEs can influence evolutionary responses to selection remains ambiguous. We tested the degree to which MEs can alter the rate of adaptation of a key life-history trait, clutch size, using an individual-based model approach parameterized with experimental data from a long-term study of great tits (*Parus major*). We modeled two types of MEs: (i) an environmentally plastic ME, in which the relationship between maternal and offspring clutch size depended on the maternal environment via offspring condition, and (ii) a fixed ME, in which this relationship was constant. Although both types of ME affected the rate of adaptation following an abrupt environmental shift, the overall effects were small. We conclude that evolutionary consequences of MEs are modest at best in our study system, at least for the trait and the particular type of ME we considered here. A closer link between theoretical and empirical work on MEs would hence be useful to obtain accurate predictions about the evolutionary consequences of MEs more generally.

Keywords: adaptation, environmental shift, evolutionary dynamics, maternal inheritance, plastic maternal effect, quantitative genetics.

Introduction

There is increasing recognition among evolutionary biologists of nongenetic (Mameli 2004; Danchin et al. 2011) or indirect genetic (Wolf et al. 1998) mechanisms of inheritance that affect the dynamics of phenotypic adaptation in populations. One such example is that of maternal effects (Mousseau and Fox 1998). In its most general sense, a maternal effect is the degree to which an offspring's phenotype is shaped by properties of the mother other than shared-genes effects, although these maternal properties may themselves have a genetic basis (Willham 1963; Mousseau and Fox 1998; Wolf et al. 1998; Bijma 2011). This can include effects of the maternal trait on the same trait in the offspring, such as litter size in mice (Falconer 1965) or age at maturity in springtails (Janssen et al. 1988), as well as the effect of maternal trait(s) on a different trait in the offspring, such as the effects of host-plant choice of the mother on offspring morphology or of egg or propagule size on offspring growth rate (Mousseau and Fox 1998; Räsänen and Kruuk 2007). This study is concerned with the former type of maternal effects. Although maternal effects are sometimes thought of as nuisance parameters hampering the prediction of evolutionary trajectories (Räsänen and Kruuk 2007; Danchin et al. 2011), theoretical models and empirical studies show that the presence of such effects can have profound impacts on rates of adaptation (Kirkpatrick and Lande 1989; Bijma 2011; Hoyle and Ezard 2012; McGlothlin and Galloway 2013).

Falconer (1965) described maternal effects, m, as a (partial) linear regression coefficient for offspring trait value on the same maternal trait value. An individual's phenotype z is then the sum of its breeding value A, its environment ε, and the partial maternal-effects regression coefficient times the mother's phenotype z_m ($z = A + \varepsilon + mz_m$). The narrow-sense heritability for the trait—that is, the proportion of total phenotypic variance attributable to additive genetic effects—may now no longer adequately capture the potential for evolution because the maternal genotype has direct (via additive genetic inheritance) and indirect (via the maternal effect) effects on offspring phenotype. This concept was used by Kirkpatrick and Lande (1989) to devise a model

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that predicts evolutionary change across generations with the incorporation of phenotypic change due to maternal effects in current and previous generations. When maternal effects are absent, this model reduces to a standard model of additive inheritance. However, when positive maternal effects are present (i.e., $m > 0$, so that a larger maternal trait value results in a larger offspring trait value), the covariance between an individual's breeding value and its trait value exceeds the additive genetic variance for that trait, which facilitates a more rapid change in the mean trait value under directional selection. Negative maternal effects (i.e., $m < 0$, so that a larger maternal trait value results in a smaller offspring trait value) can reduce the response and possibly even revert it. For example, growth rate (offspring trait) can be impaired by the amount of maternal care (maternal trait); this may have implications for offspring survival and hence the distribution of phenotypes in the next generation, causing an evolutionary time lag (Kirkpatrick and Lande 1989; Wolf et al. 1998).

Theoretical studies of maternal inheritance effects on fitness and rates of adaptation are ample (Kirkpatrick and Lande 1989; Bijma 2011; Hoyle and Ezard 2012; Prizak et al. 2014; Kuijper and Hoyle 2015). Empirical work mainly comes from short-term studies testing the effect of experimentally manipulated maternal trait values on offspring performance (e.g., Schluter and Gustafsson 1993; Beckerman et al. 2006; Rechavi et al. 2011; but for studies with more generations, see, e.g., Plaistow and Benton 2009; Dey et al. 2016), and some have identified a role for epigenetic effects as an important driver of phenotypic variation in offspring (e.g., Cubas et al. 1999; Champagne 2008). Such short-term studies are, however, insufficient to inform us about the magnitude of maternal effects at longer (micro)evolutionary timescales (i.e., at least tens of generations) in natural populations, for which evidence to date remains scarce (Räsänen and Kruuk 2007; McAdam et al. 2014). Quantitative genetic modeling in long-term observational studies of natural populations can provide insights into maternal sources of phenotypic variation but require high-quality data that are not always available (Merilä et al. 2001*a*; Kruuk and Hadfield 2007). Furthermore, if the maternal effect does not reflect a fixed maternal property but varies among breeding events, it is difficult to disentangle maternal from genetic effects. The maternal effect component mz_m on phenotype z (sensu Kirkpatrick and Lande 1989), as well as the slope and sign of m, is therefore difficult to estimate in most natural study systems without a highly informative pedigree (but see McAdam and Boutin 2004).

Typically, the role of maternal effects in evolution has been regarded as fixed, that is, assuming a constant value for m (Kirkpatrick and Lande 1989; Bijma 2011). Different scenarios can then be explored, varying m and predicting its role in adaptation and fitness in combination with other adaptive mechanisms such as phenotypic plasticity and grand-maternal effects (Hoyle and Ezard 2012; Ezard et al. 2014; Prizak et al. 2014). In reality, however, maternal effects may not be fixed but plastic in response to environmental conditions and hence may change from season to season. For example, inbred Seychelles warbler (*Acrocephalus sechellensis*) mothers produce low-quality offspring, which in turn affects offspring survival, but only in poor breeding seasons (Richardson et al. 2004). As offspring were cross-fostered in that study and common-environment effects could thus be ruled out, this suggests an environmentally plastic maternal effect mediated through the egg. Similarly, if offspring traits are condition dependent and offspring condition is in turn influenced by a maternal effect at a different rate in different environments, the net maternal effect will then be plastic; that is, the coefficient m will vary with environments. The ability of m to vary with the environment means that there can be differential selection on the maternal component of the phenotype in different environments, and if the maternal trait is under genetic control, this may hence considerably alter evolutionary trajectories (Kuijper and Hoyle 2015).

Avian clutch size, a major life-history trait, is highly variable in some species, and this variability has a genetic basis (Postma and van Noordwijk 2005). Stabilizing selection on clutch size is likely to be strong, as deviations from the optimal clutch size compromise offspring viability and recruitment and, therefore, maternal fitness (Pettifor et al. 1988, 2001; Krementz et al. 1989; Both et al. 1999, 2000; Rodríguez et al. 2016). The maternal effect of the mother's clutch size on her daughters' clutch size is a likely candidate for an environmentally plastic maternal effect, as maternal clutch size affects offspring body condition, depending on the environment, and offspring condition likely affects offspring clutch size. Females that lay clutches larger than their individual optima produce offspring of relatively poor condition (Sanz 1997; Both et al. 2000; Pettifor et al. 2001). If this poor condition persists through to breeding age, then these offspring in turn will lay smaller clutches than predicted by the genes inherited from their parents, because the number of eggs a bird can produce is condition dependent (e.g., Schluter and Gustafsson 1993; but see Merilä et al. 2001*a*). Their offspring (i.e., the grand-offspring of the original females), now born in clutches that are too small (i.e., a clutch size smaller than the number of young that could be successfully raised), will be relatively heavy because food is shared among fewer nestlings and may in turn go on to lay (too) large clutches as adults (Haywood and Perrins 1992; Tilgar et al. 2010; but see Haywood 2013). This effect may perpetuate through the generations, although it should wane quickly in stable environments as the phenotype is pulled toward the optimum (cf. Kirkpatrick and Lande 1989; Bijma 2011).

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The environmentally plastic nature of *m* becomes apparent when considering the environment-dependent relationship between maternal clutch size and resulting fledgling weight: as there is a trade-off between offspring quantity and quality, offspring fledgling weight will decrease more strongly with maternal clutch size under adverse conditions rather than favorable conditions (e.g., when food is abundant; Both et al. 2000). The maternal effect will therefore vary with the environment, and this has the potential to change the rate of adaptation of a population when it is under directional selection. Adaptation dynamics could be affected in two ways: offspring that fledge in poor condition may survive less well, and those that do survive may produce smaller clutches as adults. Either or both would therefore affect the total strength of selection on maternal clutch size. To predict this in a model, one would therefore need to estimate four important parameters: (i) the narrow-sense heritability of clutch size, (ii) the environment dependency of the clutch size–offspring condition relationship, (iii) survival based on offspring condition as a selection factor on maternal clutch size (note that for the sake of simplicity, this disregards viability selection operating on adults), and (iv) the effect of offspring condition on offspring clutch size (see fig. 1).

In this article, we addressed the question of to what extent environmentally plastic maternal effects can speed up or slow down the rate of adaptation of clutch size in a wild population using empirically estimated parameter values. We estimated the parameters for an exceptionally well-studied passerine bird, the great tit (*Parus major*), to calculate both environmentally plastic and fixed maternal effects. These were then used in an individual-based model to predict the rate of adaptation of clutch size following an environmental shift. We estimated maternal effects by regressing offspring phenotype on maternally induced offspring condition or maternal phenotype, using a combination of long-term field observations and multiyear experimental manipulations (Both et al. 2000). In keeping with theoretical findings concerning environment-dependent maternal effects (Hoyle and Ezard 2012; Kuijper and Hoyle 2015), we explored two alternative, but related routes toward quantifying maternal effects: (i) via fledgling weight, which itself is a result of maternal clutch size and the environment (mak-

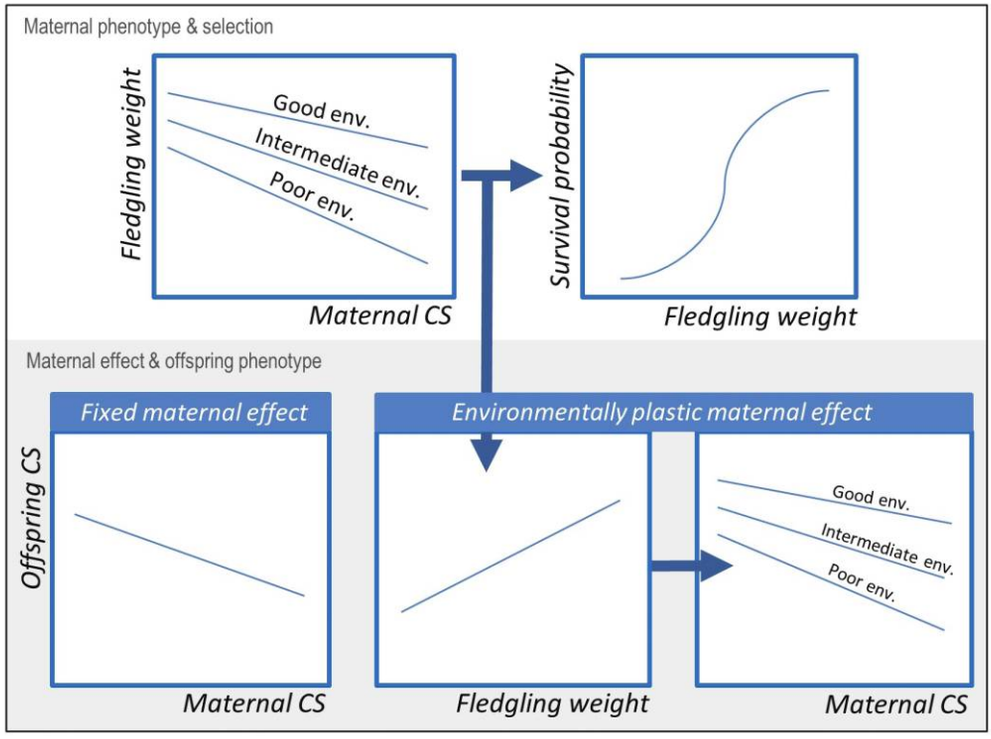


Figure 1: Two alternative approaches to estimating maternal effects underlying avian clutch size. Maternal clutch size (CS) affects offspring condition (weight) depending on the quality of the environment, and this condition in turn drives selection through offspring survival (*top row*). In one scenario, offspring condition also affects their phenotype (clutch size), which when regressed against the maternal CS results in an environmentally plastic maternal effect (*bottom right*). Alternatively, the maternal CS directly influences offspring CS independent of the environment, resulting in a fixed maternal effect (*bottom left*).

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ing m environmentally plastic); and (ii) via a fixed maternal effect (i.e., using the conventional definition of m), where m is not environment dependent (fig. 1). Although conceptually simplified, the latter effect may arise, for example, as a result of brood size–mediated androgen levels that may negatively affect offspring fecundity (Naguib et al. 2004; Rutkowska et al. 2005) or transgenerational epigenetic inheritance induced by maternal malnutrition (Champagne 2008; Jablonka and Raz 2009). We explicitly used parameters from a wild population to explore realistic evolutionary responses in a key life-history trait under reasonably strong directional selection.

Methods

Study System

We estimated our model parameters from data from a long-term (1955–present) population study of great tits (*Parus major*), a hole-breeding passerine, at the Hoge Veluwe National Park in the Netherlands (lat. 52°02′07″N, long. 5°51′32″E). The 171-ha study area, comprising a mixture of deciduous and coniferous forest stands, has ~400 nest boxes that are checked weekly from April to July to score life-history traits including egg-laying/-hatching date and clutch size. When nestlings are 7–8 days old, the parents are captured in their nest boxes (using spring-door traps), banded, and blood sampled; nestlings are banded, blood sampled, and weighed at day 15, which is close to the age of fledging. The banding of birds allows for carefully monitoring immigration and offspring recruitment and establishing pedigrees. The study area is surrounded by a matrix of potentially suitable breeding habitat, which facilitates dispersal from and into the focal area. The population has been studied continuously since 1955 and has been subjected to various experiments aimed at manipulating life-history traits such as egg-laying date and clutch size.

The Individual-Based Model

We used an individual-based model to estimate the impact of (environmentally plastic) maternal effects on adaptation. Population size N was roughly 500 in every model generation, assuming no overlapping generations (i.e., the whole adult population is replaced by recruits every year). In each generation, a sex (ratio 1 : 1) was randomly assigned to individuals, and both sexes were paired up randomly for mating. We simulated a total of 1,000 generations—that is, 500 burn-in generations to reach equilibrium conditions, followed by an environmental shift and 500 additional generations—and repeated the process 1,000 times. To avoid confusion, we refer to clutch size and fledgling weight as z_{CS} or z_{FW}, respectively, throughout. Parameters requiring estimation from data are summarized in tables 1 and 2. An example script of the model for the R environment has been uploaded as supplementary material.

Generating a Population, Genotypes, and Phenotypes. The clutch size of a given individual (i) in the initial population was defined as

$$z_{\mathrm{CS}_i} = \mu_{\mathrm{CS}} + A_{\mathrm{CS}_i} + M_{\mathrm{CS}_i} + \varepsilon_i, \quad (1)$$

where μ_{CS} is a constant (here, 8.0), A_{CS_i} is the individual's genotype (breeding value), M_{CS_i} is its maternal component (i.e., mz_m, as in Falconer 1965), and ε_i is the residual component, all initially randomly drawn from a univariate normal distribution with mean 0 and standard deviations $(V_{A_{\mathrm{CS}}})^{1/2}$, $(V_{M_{\mathrm{CS}}})^{1/2}$, and $(V_{z_{\mathrm{CS}}} - V_{A_{\mathrm{CS}}} - V_{M_{\mathrm{CS}}})^{1/2}$, respectively. For all following generations, z_{CS_i} was calculated as in equation (1), but A_{CS_i} and M_{CS_i} were no longer randomly drawn but calculated from parameter values in the current generation. Offspring genotype was defined as

$$A_{\mathrm{CS}_i} = \frac{A_{\mathrm{CS}_{\mathrm{mother}_i}} + A_{\mathrm{CS}_{\mathrm{father}_i}}}{2} + y_i, \quad (2)$$

where y_i is the Mendelian segregation error, drawn from a univariate normal distribution with mean 0 and standard deviation $(0.5\,V_{A_{\mathrm{CS}}})^{1/2}$ (Lynch and Walsh 1998).

Maternal Effect. Here, we assumed two types of maternal effects: (i) an environmentally plastic effect via fledgling weight, determined by maternal clutch size in interaction with the environment, and (ii) a fixed effect that depends only on maternal clutch size. In the case of the environmentally plastic maternal effect, M_{CS_i} is calculated as

$$M_{\mathrm{CS}_i} = \alpha_p + \beta_p z_{\mathrm{FW}_i}, \quad (3)$$

where α_p and β_p—the subscript p referring to a plastic maternal effect—are the intercept and slope (i.e., partial regression coefficient), respectively, from a regression of offspring clutch size on offspring fledgling weight z_{FW_i} (estimated while controlling for additive genetic effects; see "Estimating Model Parameters from Data").

The fixed (f) maternal effect is calculated from the maternal clutch size $z_{\mathrm{CS}_{m_i}}$ as

$$M_{\mathrm{CS}_i} = \alpha_f + m_f z_{\mathrm{CS}_{m_i}}, \quad (4)$$

where α_f and m_f are the intercept and slope (i.e., a partial regression coefficient) from a regression of offspring clutch size against maternal clutch size (estimated while controlling for both fledgling weight and additive genetic effects; see "Estimating Model Parameters from Data"). Both types of maternal effects were run in separate models (i.e., containing either only the plastic or only the fixed type), where

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Table 1: Summary of input parameters for the individual-based model, estimated from the great tit population at the Hoge Veluwe National Park

Parameter, mixed model component	Estimate	SE	Notation	Details
Heritability CS	.24	.04	h^2_{CS}	Table S1
Fledgling weight as function of CS and environment (year):[a,b]				Table S2; eq. (5)
1988 (poor environment)	.53	.06	α_{FW_j}	
1984 (intermediate environment)	.49	.05	α_{FW_j}	
1986 (good environment)	.81	.05	α_{FW_j}	
1988 : CS	−.30	.06	β_{FW_j}	
1984 : CS	−.08	.01	β_{FW_j}	
1986 : CS	−.06	.01	β_{FW_j}	
Offspring survival:[a]				Table S3; eq. (6)
Intercept	−19.06	2.92	α_ϕ	
Fledgling weight	1.62	.33	β_ϕ	
[Fledgling weight]^2	−.04	.01	γ_ϕ	
Maternal effect:				
Via fledgling weight:[b,c]				Table S4; eq. (3)
Intercept	−.25	.06	α_p	
Fledgling weight	.13	.05	β_p	
Coefficient for M_{CS_i} against $z_{CS_{m_i}}$:				
Poor environment	−.13	…	m_p	
Intermediate environment	−.04	…	m_p	
Good environment	−.03	…	m_p	
Via maternal CS:[b]				Table S5; eq. (4)
Intercept	−.25	.06	α_f	
Maternal CS	−.21	.03	m_f	

Note: Shown are estimates of intercepts and slopes (and their standard errors) from mixed-effects models detailed in the supplementary tables. CS = clutch size.

[a] Estimates are on a logit scale.

[b] Continuous predictor variables were centered around their annual mean before analysis and decentered in the individual-based model.

[c] Implicit maternal-effects coefficient m_p is derived by regressing the maternal component M_{CS_i} (eq. [3]) on environment-specific maternal clutch size z_{CS_m}; $\beta_p = 0.10$ (± 0.04 SE) in the model combining fixed and plastic maternal effects.

their effect on the rate of adaptation was determined by keeping M_{CS_i} in or removing it from equation (1).

As equation (3) models M_{CS_i} as a function of fledgling weight, β_p has to be positive. To intuitively compare both types of maternal effect, we regressed M_{CS_i} resulting from equation (3) on maternal clutch size $z_{CS_{m_i}}$ for each environment to obtain a negative (partial) regression coefficient m_p associated with each environment. Note that m_p was merely

Table 2: Additional model input parameters for the initial population

Description	Notation	Estimate	Details
Phenotypic variance[a]	$V_{z_{CS}}$	3.91	…
Additive genetic variance	$V_{A_{CS}} (= h^2_{CS} \times V_{z_{CS}})$	.94	…
Relative maternal effect variance:[b]			
For m_p model[c]	M^2_{CS}	.006	Table S4
For m_f model	M^2_{CS}	.027	Table S5
Maternal effect variance:			
For m_p model	$V_{M_{CS}} (= M^2_{CS} \times V_{z_{CS}})$[d]	.02	…
For m_f model	$V_{M_{CS}} (= M^2_{CS} \times V_{z_{CS}})$	.11	…

Note: CS = clutch size.

[a] Estimated from the Hoge Veluwe population.

[b] Calculated using Nakagawa and Schielzeth's (2013) marginal R^2 for mixed-effects models.

[c] In the model combining fixed and plastic maternal effects, this value was 0.003 (table S5).

[d] In the model combining fixed and plastic maternal effects, this value was 0.01.

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estimated for illustrative purposes; in the model, m_p was incorporated implicitly via the effect of fledgling weight as in equation (3).

The combined effect of both maternal effects, both represented by partial regression coefficients (see "Estimating Model Parameters from Data"), was tested in a third model that was defined by extending the maternal-inheritance component in equation (1) as M_{CS_i} (eq. [3]) + M_{CS_i} (eq. [4]; i.e., combining both the plastic and the fixed types in a single model).

Fledgling Weight, Survival, and Fitness. Offspring fledgling weight z_{FW_i} is a function of maternal clutch size $z_{\mathrm{CS}_{m_i}}$. Since fledgling weight is in nature bounded between a minimum and a maximum, it was modeled as a linear function of maternal clutch size assuming a logit scale; this allowed for back transformation to get a naturally sigmoidal, asymptotic relationship (see "Estimating Model Parameters from Data"). Fledgling weight before back transformation was defined as

$$z'_{\mathrm{FW}_i} = \alpha_{\mathrm{FW}_j} + \beta_{\mathrm{FW}_j} z_{\mathrm{CS}_{m_i}}, \tag{5}$$

where α_{FW_j} and β_{FW_j} are the intercept and slope related to the jth environment. Fledgling weight z_{FW_i} (calculated as $e^{z'_{\mathrm{FW}_i}}/[1 + e^{z'_{\mathrm{FW}_i}}] \times [\max - \min] + \min$, with max and min indicating predefined boundaries) affects offspring survival (recruitment) probability, ϕ_i, according to the logistic function

$$\phi_i = \frac{1}{1 + e^{-(\alpha_\phi + \beta_\phi z_{\mathrm{FW}_i} + \gamma_\phi z_{\mathrm{FW}_i^2})}}, \tag{6}$$

where α_ϕ and β_ϕ are the fledgling weight-related intercept and slope; γ_ϕ is the negative slope associated with the quadratic term, as survival was expected to level off and eventually decrease at extremely high fledgling weights (Mulder et al. 2016). A mother's fitness, W_i, is the product of her clutch size and offspring survival probability, yielding

$$W_i = z_{\mathrm{CS}_i} \phi_i. \tag{7}$$

Note that the index i for offspring survival probability ϕ_i is still useful here as all offspring from the same brood are expected to have the same value for ϕ_i. Then W_i is scaled up to match the number of recruits that need to be produced to reach N:

$$W'_i = W_i \frac{\overline{n}_{E_i}}{\overline{W}}, \tag{8}$$

where $\overline{n}_{E_i}$ is the expected mean number of recruits produced per brood pair and $\overline{W}$ is the average fitness over all broods. The actual number of recruits produced by each brood, n_i, is then determined by randomly drawing from a Poisson distribution with $\lambda_i = W'_i$. To quantify the strength of selection, the standardized selection differential (s) for a given year (j) was calculated following Lande and Arnold (1983):

$$s_j = \frac{\mathrm{cov}[(n_{ij}/\overline{n}_j), z_{\mathrm{CS}_{ij}}]}{\sigma_{z_{\mathrm{CS}_j}}}, \tag{9}$$

where $\overline{n}_j$ is the average number of recruits per brood and $\sigma_{z_{\mathrm{CS}_j}}$ is the standard deviation of z_{CS_j}.

Environmental Change. To allow model parameters to equilibrate before the stepwise change in the environment, we ran the model in an intermediate environment for 500 generations. After this burn-in period, the environment switched to either a poor or a good environment by either increasing (good environment) or decreasing (poor environment) α_{FW_j} and β_{FW_j} in equation (5) (note that because β_{FW_j} is negative, a higher value means a shallower slope). This means that the population moved to different fitness optima, as the relationship between maternal clutch size and offspring fledgling weight (eq. [5]) differed among different environments. The environmental shift was abrupt (i.e., during one generation) and was kept constant for another 500 generations.

Estimating Model Parameters from Data

Four analyses were performed to estimate four parameters necessary for our individual-based model: (i) heritability of clutch size, (ii) the environment-dependent effect of maternal clutch size on fledgling weight, (iii) the effect of fledgling weight on offspring recruitment, and (iv) the maternal effect, that is, the effect of fledgling weight and/or maternal clutch size on offspring clutch size. All relevant parameters are summarized in tables 1 and 2; data have been deposited in the Dryad Digital Repository: https://doi.org/10.5061/dryad.4fv71 (Ramakers et al. 2018).

Heritability of Clutch Size. To estimate heritability, we used all unmanipulated first clutches from all birds from 1956 to 2013 with known identity (n = 5,394 observations from 3,328 females). We modeled clutch size in an animal model (Henderson 1988; Kruuk 2004) with Gaussian errors, based on restricted maximum likelihood estimation using ASReml-R, version 3 (Gilmour et al. 2009). Fixed effects were age (first-time breeder or older), egg-laying date (centered around the mean value for that year), and year of breeding (as a factor); random effects were female identity (permanent environment), maternal identity, nest box identity, and the additive genetic component based on the pedigree. Males do not express a clutch size phenotype, but it was assumed here that they carry the genes for clutch size, and hence paternal links were included in the analysis. In the construction of the pedigree, the female's social partner was assumed the genetic father. Molec-

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ular analysis in a nearby great tit population has revealed that the proportion of extrapair young ranges from 6.5% to 12.5% (van Oers et al. 2008). Such rates are common for tit species (Brommer et al. 2010) but have been found to only marginally affect heritability estimations when sample sizes are sufficiently large (i.e., >100; Charmantier and Réale 2005).

All fixed and random variables contributed significantly to variation in clutch size, with the exception of maternal identity (table S1; tables S1–S5 are available online). Narrow-sense heritability (h^2_{CS}) was estimated at 0.24 (± 0.04 SE).

Fledgling Weight Versus Maternal Clutch Size. To estimate the environment-dependent effect of clutch size on fledgling weight, we cannot rely on observational data since different females likely have different, individually optimized clutch sizes (Pettifor et al. 1988, 2001). We therefore made use of 8 years (1983–1990) of brood size manipulations at our study site (Both et al. 2000) to estimate α_{FW_j} and β_{FW_j} in equation (5). Briefly, each year, triplets were formed of nests with the same clutch size and hatching date, within which broods were randomly chosen to be either enlarged or reduced by approximately a half or to remain the same size when chicks were 1–3 days old. The year 1988 differed somewhat in that three broods of different sizes were manipulated to one common brood size. Our aim was to find year-dependent trade-offs between a female's clutch size and her offspring's body condition. Different years are here assumed to represent different environments, that is, in terms of food availability or breeding-pair densities, with poor years exhibiting the steepest negative slope of fledgling weight versus clutch size and a comparatively low average body condition. We therefore modeled fledgling weight ($n = 2{,}145$ nestlings) as a function of manipulated brood size, year, and the interaction between the two, as well as original clutch size and hatching date, in a linear mixed-effects model using the R package lme4 (Bates et al. 2015); brood identity ($n = 309$) nested within female identity ($n = 251$) served as a random effect. All continuous predictor variables were centered around their mean value for that year; fledgling weight was transformed to a logit scale before analysis ($z'_{\mathrm{FW}_i} = p/[1-p]$, where $p = [z_{\mathrm{FW}_i} - 5.5]/[22.5 - 5.5]$) to allow for realistic asymptotes at both extremes of the weight spectrum (i.e., $5.5\ \mathrm{g} < z_{\mathrm{FW}} < 22.5\ \mathrm{g}$) after back transformation. Manipulated brood size, year, and their interaction were highly significant (table S2): years differed in both elevation and slope of the clutch size–fledgling weight relationship (fig. S1; figs. S1–S6 are available online). We chose three particular years to represent good, intermediate, and poor environments (fig. 2) based on the values for α_{FW_j} (the weight in the average environment) and β_{FW_j} (the steepness of the curve, with the shallower slopes indicating better environments). We chose 1988 to represent the poor environment; note that although the experimental procedure in this year differed somewhat from other years and 1988 might thus be an oddity, its steep slope renders it a suitable extreme scenario.

Offspring Survival Probability. We modeled offspring survival probability ϕ based on recruitment probability (which approximates survival) as a function of fledgling weight and the square of fledgling weight. We thus ran a generalized linear mixed-effects model with a logit link to estimate α_ϕ, β_ϕ, and γ_ϕ (eq. [6]). Fledglings could either return or not return to the breeding population (1/0 response). Brood identity nested within year of breeding was added as a random effect. We used data from 1973–2013 because of few observations in earlier years ($n = 24{,}320$ nestlings from 3,600 broods). Recruitment probability showed a highly significant, quadratic response to fledgling weight (table S3) and was approximately constrained below 0.1 (fig. 3). We also tested whether fledgling weight interacted with year (i.e., whether β_ϕ varied among years) but found no statistical evidence for this (results not shown).

Maternal Effect on Offspring Clutch Size. To estimate the maternal effect on offspring clutch size, we explored two

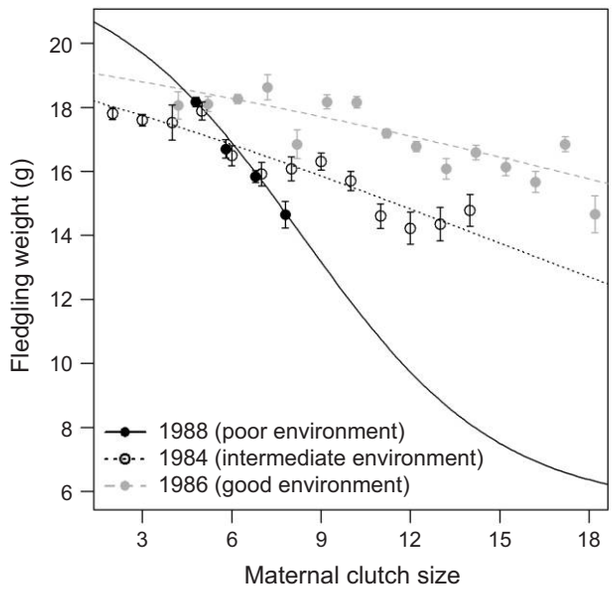


Figure 2: Great tit fledgling mass at the Hoge Veluwe National Park as a function of maternal clutch size for three representative (good, intermediate, and poor) years. Means and standard errors (with slight horizontal spacing added between years) are given for visual purposes only. Trend lines are back-transformed estimates from a linear mixed-effects model with fledgling weight on a logit scale and clutch size originally mean centered (tables 1, 2, S2), extrapolated beyond the data range to illustrate their range within the individual-based model. Note that clutch sizes are actually experimentally manipulated brood sizes; 1988 had few manipulated brood sizes compared to other years because in this year the manipulation procedure was slightly different (Both et al. 2000).

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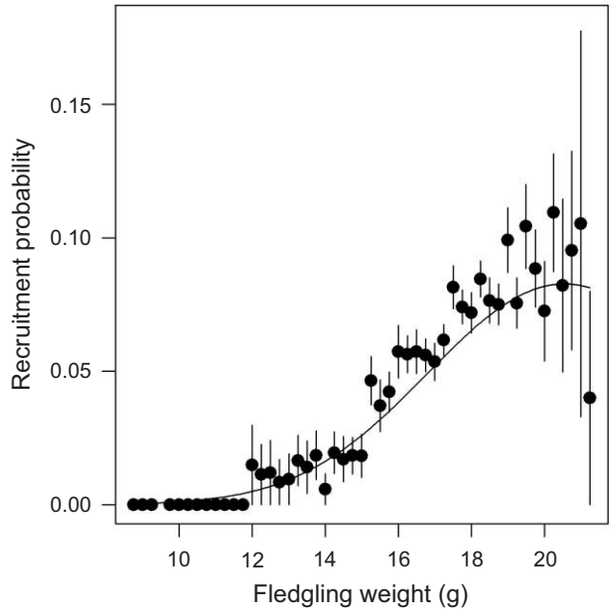


Figure 3: Recruitment probability of great tits at the Hoge Veluwe National Park as a function of their fledgling weight (see tables 1, 2, S3). Means and their standard errors are given for visual purposes only, and extreme fledgling weights (at both ends of the spectrum) were disregarded due to too few observations.

routes: one that acts through offspring fledgling weight and where it is environmentally plastic (eq. [3]), and one that acts through maternal clutch size and is not environmentally plastic (eq. [4]). From the 1973–2013 data set, we extracted all first-year breeding attempts of females with known fledgling weights and known mothers ($n = 510$). As clutch size is partly under genetic control, we needed to account for this effect when estimating effects of fledgling weight or maternal clutch size on offspring clutch size. To do this, we used the predicted breeding values (PBVs) extracted from the previous animal model (i.e., best linear unbiased predictions) based on the complete data set. We are fully aware that PBVs can come with substantial and potentially nonrandom prediction errors (Hadfield et al. 2010), but the data set used to estimate the maternal effect was too small to estimate additive genetic variance reliably, and we are convinced that this approach gives more reliable results. Note that, consequently, our estimates of negative maternal effects are likely somewhat conservative (i.e., show an upward bias) given the positive association between maternal and offspring phenotypes expected from genetic inheritance.

In the first model, maternal clutch size affected offspring clutch size via fledgling weight, which makes it an environmentally plastic effect since the effect of maternal clutch size on fledgling weight varies with the environment (figs. 2, 4*b*). Fledgling weight and PBV significantly contributed to variation in offspring clutch size, the former explaining 0.6% of variation and having an estimated slope (β_p) of 0.13 eggs g^{-1} (tables 1, 2, S4; fig. 4*a*). To obtain m_p, which is only implicitly modeled, we subsequently regressed M_{CS_i} against maternal clutch size, which led to three different, environment-dependent values for m_p approximately corresponding to -0.13, -0.04, and -0.03 for poor, intermediate, and good environments, respectively (see fig. 4*b*; note that these curves are nonlinear).

In the second model, the maternal effect was estimated as the partial regression coefficient for offspring against maternal clutch size (m_f) and was not environmentally plastic (eq. [4]). A similar mixed-effects model was run, but maternal clutch size z_{CS_m} (centred around the annual mean value) was added, as well as its interaction with mean population fledgling weight in the current breeding year t ($\overline{z}_{\mathrm{FW}_t}$), as a measure of environmental quality, to assess whether the effect of maternal clutch size on offspring clutch size depended on the environment. Besides PBV and individual fledgling weight (z_{FW_i}), maternal clutch size was highly significant and explained 2.7% of variation (tables 1, 2, S5; fig. 4*c*); the maternal-effects coefficient was estimated at $m_f = -0.21$ (note that in this model the effect of fledgling weight [β_p] was reduced to 0.10 eggs g^{-1}, explaining 0.3% of variation). There was no significant effect of $\overline{z}_{\mathrm{FW}_t}$, nor was there an interaction between z_{CS_m} and $\overline{z}_{\mathrm{FW}_t}$, reinforcing the view that m_f is not environmentally plastic.

Results

Environmentally Plastic Maternal Effects ($\mathrm{m_p}$)

Environmentally plastic maternal effects only marginally affected the rate of adaptation following an environmental shift to new phenotypic optima, relative to the situation where maternal effects were absent (fig. 5*a*, 5*b*; see fig. S3 for changes in mean maternal effects component $\overline{M}_{\mathrm{CS}}$, phenotypic variance $\overline{V}_{z_{\mathrm{CS}}}$, fledgling weight $\overline{z}_{\mathrm{FW}}$, and selection differential $\overline{s}$).

Under selection for a larger clutch size, offspring survival probability increased after the environmental shift—regardless of maternal clutch size. This is because fledgling weight was little compromised when clutches were large in the new, good environment (fig. 2; see also $\overline{z}_{\mathrm{FW}}$ in fig. S3). Surviving offspring in the first generation following the environmental shift, many of them in relatively good condition, laid relatively large clutches that did not result in a reduction of offspring weight. Therefore, a negative m_p coefficient slightly favored adaptation in the first 100 years following the burn-in. As the new optimum trait value was approached, selection decreased (fig. S3), hence diminishing the response in $\overline{z}_{\mathrm{CS}}$ compared to the scenario without a maternal effect from ~70 years onward.

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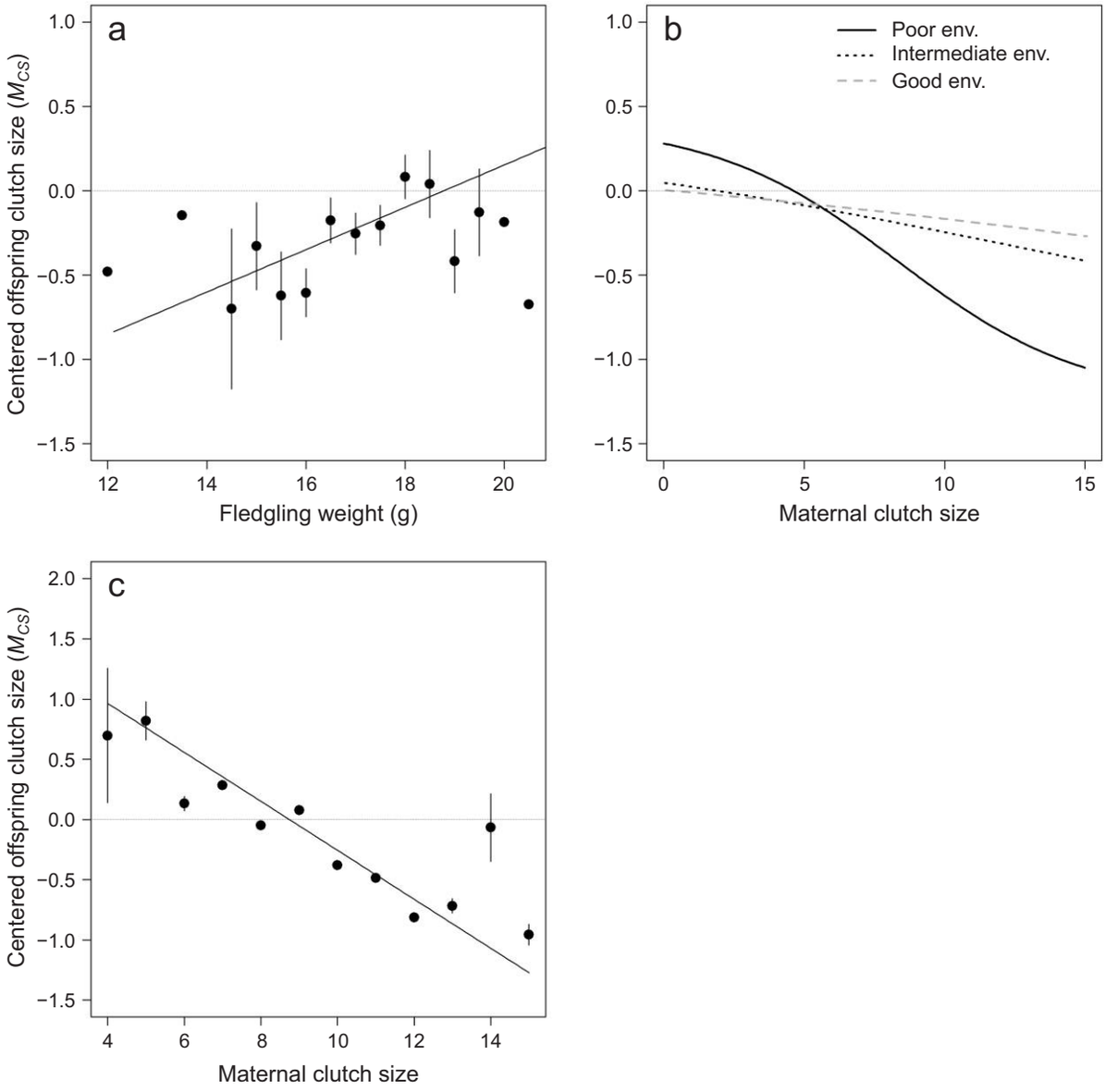


Figure 4: Maternal effect on offspring clutch size in great tits at the Hoge Veluwe National Park. The environmentally plastic maternal effect operates through fledgling weight (*a*); plotting the resulting centered maternal clutch size (i.e., the maternal-effects component M_{CS}) against the maternal phenotype in the mother's environment leads to three environment-specific maternal effects m_p (*b*). The fixed maternal effect m_f is the effect of maternal clutch size on offspring clutch size independently of fledgling weight and is not environmentally plastic (*c*). Points are means and their standard errors, corrected for predicted breeding values (PBVs), given for visual purposes only. Lines are estimates from linear mixed-effects models, keeping PBVs constant at their mean (tables S4, S5).

Under selection for smaller clutch size in the poor environment, which was much stronger than the selection for larger clutch size because of the narrower fitness peak (figs. S2, S3, S6), the initially enhancing effect of a negative m_p coefficient was more pronounced but lasted much shorter. After the environmental shift selecting for smaller clutch size, individuals laid too large clutches, resulting in a low average fledgling weight in generation t and, consequently, a drop in $\overline{z}_{CS}$ in year $t + 1$. The fixed weight–survival curve (fig. 3) ensured that only the heaviest offspring survived (fig. S3), which in turn would lay relatively large clutches—hence the slight upward tilt following generation $t + 2$. Again, the negative m_p coefficient pushed $\overline{z}_{CS}$ in the wrong direction, resulting in a lagged response compared to the scenario without a maternal effect from generations 7–8 onward (fig. 5*a*, insets).

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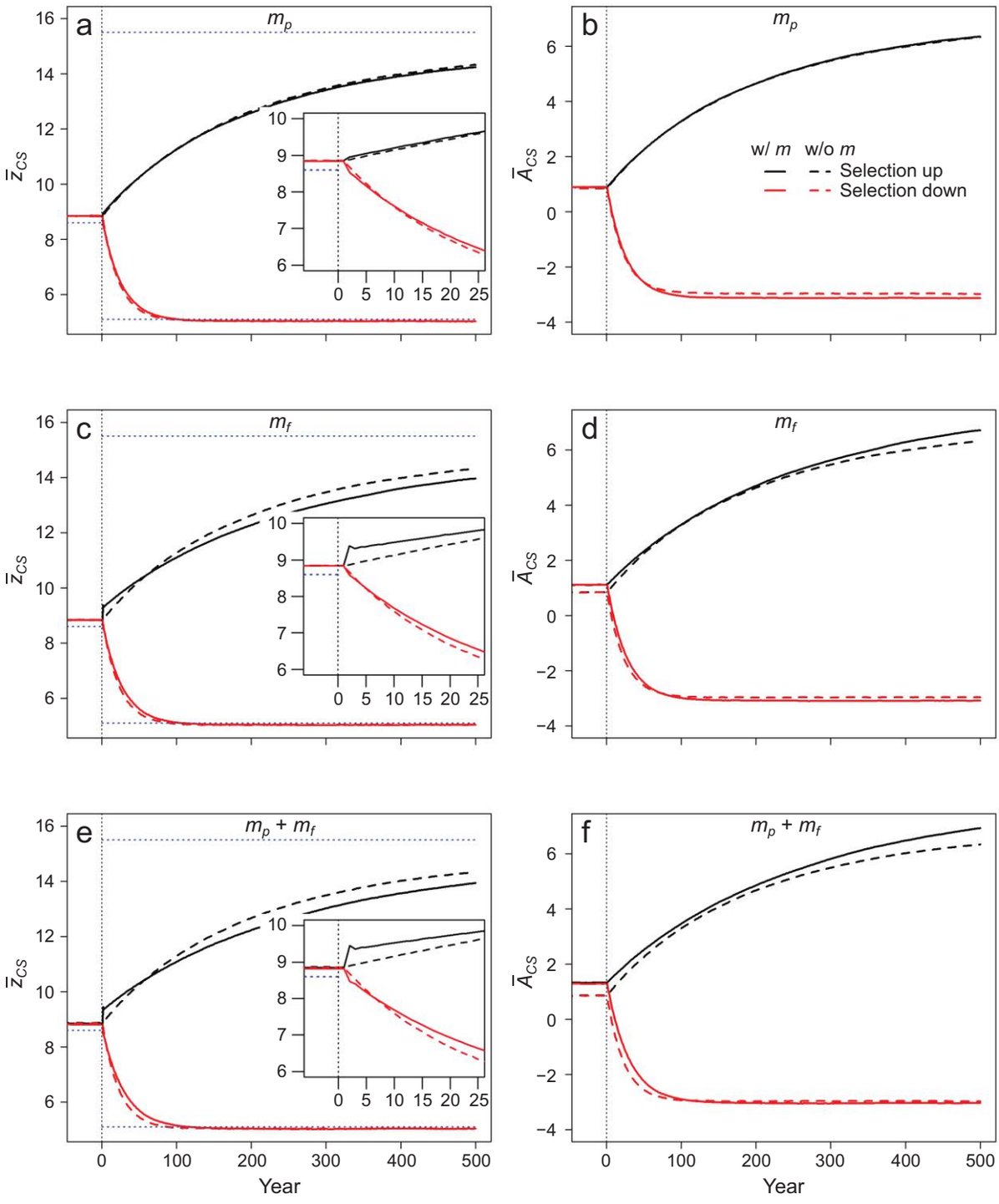


Figure 5: Predicted mean phenotypic (*a*, *c*, *e*) and genetic (*b*, *d*, *f*) change in avian clutch size (modeled after the great tit at the Hoge Veluwe National Park) in response to selection when considering a realistic environmentally plastic (i.e., via fledgling weight; *a*, *b*), fixed (i.e., via maternal clutch size; *c*, *d*) or combined (*e*, *f*) maternal effect (solid lines), or no maternal effect at all (dashed lines). Phenotypic responses in the first 25 years are magnified in the insets in *a*, *c*, and *e*. The vertical line denotes the pre-burn-in period, after which selection moves from an intermediate clutch size to either a large (good environment) or small (poor environment) clutch; the blue dotted lines in *a*, *c*, and *e* denote the optimal phenotype, that is, z_{CS} at W_{max}. Lines are the means of population averages over 1,000 simulation runs. Input parameters are as follows: $V_{z_{CS}} = 3.91$; $h^2_{CS} = 0.24$; $M^2_{CS} = 0.006$ (*a*, *b*) or 0.003 (*e*, *f*) for the model with the plastic maternal effect; $M^2_{CS} = 0.027$ for the model with the fixed maternal effect; $m_p \approx -0.13$, -0.04, and -0.03 (depending on the environment; *a*, *b*) or -0.10, -0.03, and -0.02 (*e*, *f*); $m_f = -0.21$ (see text and tables 1, 2 for details).

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The overall effect of the environmentally plastic maternal effect, however, remained small at <0.1 eggs under selection for both larger and smaller clutches compared to the situation without the maternal effect. To illustrate the nature of the environmentally plastic maternal effect more clearly, we ran another set of models where we set the regression coefficient for offspring clutch size against fledgling weight (β_p) to a less realistic 0.5 (resulting in an implicit regression coefficient m_p of −0.52, −0.16, or −0.09 in poor, intermediate, and good environments, respectively; see "Methods"), while keeping the intercept α_p the same. These parameter settings clearly show the potential capacity of the environmentally plastic maternal effect to drive $\overline{z}_{CS}$ and $\overline{A}_{CS}$ (fig. S5*a*, S5*c*).

Fixed Maternal Effects (m_f)

In the models in which the maternal effect was fixed, offspring clutch size was independent of fledgling weight, yet the effect of the fixed maternal effect was stronger than that of the environmentally plastic maternal effect (tables 1, 2, S5). In the first generation following the environmental shift that selected for larger clutch size, the negative impact of the fixed maternal effect was alleviated as there was little cost to an intermediate clutch size; this ensured that the next generation ($t + 1$) could lay large clutches that were immediately penalized in the subsequent generation ($t + 2$; fig. 5*c*; see also fig. S4). Note that this pattern is reminiscent of an effect of offspring condition on phenotype as in the scenario of the environmentally plastic maternal effect, yet the fixed maternal effect acted independently of the effect of fledgling weight (table S5). Under selection for smaller clutches, the negative maternal effect led to a decreased response (i.e., too large clutch sizes), resulting in a lag effect from the first or second generation onward. Note that the initial, adaptive effect of the environmentally plastic maternal effect was less pronounced here, as the strong weight-dependent selection did not affect the phenotype.

The immediate effect of the fixed maternal effect compared to the model without the maternal effect was around 0.6 eggs in the first generation under selection for larger clutches, but this effect waned after a few generations and never exceeded 0.6 eggs in subsequent generations. Like in the environmentally plastic maternal effect model, therefore, the overall effect of a fixed maternal effect also remained small. Again, an exaggerated decrease of the coefficient m_f (eq. [4]) from −0.21 to −0.5 (but keeping the intercept α_f the same) in an additional set of model runs led to a more distinct effect on adaptation (i.e., adaptive under selection for larger clutches in the short run and maladaptive under both selection scenarios in the long run) and magnified the oscillations observed in the first few generations under selection for larger clutches (fig. S5*b*, S5*d*).

Combining Environmentally Plastic and Fixed Maternal Effects ($m_p + m_f$)

As the most likely scenario in our great tit study population, the third model that we considered used m_p and m_f as two separate, additive maternal effects, with parameters for both effects taken from table S5 (implicit $m_p \approx -0.10$, −0.03, or −0.02 for poor, intermediate, and good environments, respectively; $m_f = -0.21$). This model combined the relatively strong, initially enhancing effect of m_f under selection for larger clutches and the relatively strong, initially enhancing effect of m_p under selection for smaller clutches. Combined, the overall effect of m on $\overline{z}_{CS}$ and $\overline{A}_{CS}$ under selection for smaller clutches was slightly increased (fig. 5*e*, 5*f*) compared to the model with the fixed maternal effect only, but the likely effect in our study population would remain small, making a difference of <0.5 eggs in the average phenotype between models with and without maternal effects in any generation.

Discussion

Using an individual-based model, parameterized with experimental data from a long-term population study of great tits, we investigated how a specific type of maternal effects—a maternal trait affecting the same trait in the offspring—could affect the rate of adaptation in a population experiencing an environmental shift. We found that the presence of environmentally plastic or fixed (negative) maternal effects in avian clutch size can speed up phenotypic adaptation in the short run and slow it down in the long run, but their effects in real populations are likely very small. This is because the real maternal-effects coefficients—and hence explained variation—were small (tables 1, 2, S4, S5). Indeed, the use of higher values for the strength of the maternal effect showed that the model we used resulted in the familiar oscillating pattern in $\overline{z}_{CS}$ over time (fig. S5), as predicted from earlier models that incorporated negative maternal effects (Kirkpatrick and Lande 1989; Bijma 2011). Had we included a realistic adult survival rate (for great tits circa 0.5) in the model, the effect of the maternal effect on the evolutionary response would have been even more reduced due to increased generation time, indicating even more strongly that the evolutionary consequences of the maternal effect on clutch size in our population are negligible. Indeed, had we used extreme parameter values used in theoretical model exercises (e.g., Hoyle and Ezard 2012; Ezard et al. 2014; Prizak et al. 2014), the effects would have been more profound (fig. S5).

A key parameter in our stochastic model was the experimentally derived relationship between clutch size and fledgling weight, as (i) this determined the environmentally plastic maternal effect and (ii) selection on clutch size was largely

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driven by this relationship. Predicting these environmental scenarios would not have been possible with observational data, as individual optimization of clutch size (Pettifor et al. 1988, 2001) will render the among-individual relationship of fledgling weight against clutch size flat or even positive. The different relationships depicted in figure 2 are likely the direct result of population density-dependent food availability in the respective years (Both et al. 2000). By its nature, therefore, the negative slope of the relationship is steepest in poor environments, resulting in strong directional selection for smaller broods as the environment shifts from intermediate to poor (figs. S3, S4); in the good environment, the relationship is much shallower and selection is much weaker (see fig. S6). This imbalance in the strength of selection ensures that, in our model, adaptation is always faster toward smaller versus larger clutches. An initially increased response under selection for smaller clutches in the presence of the environmentally plastic maternal effects (figs. 5*a*, 5*e*, S5*a*) is then merely a result of selection acting against heavy individuals laying too large clutches, which, indeed, is rapidly counteracted in subsequent generations.

The best (empirical) model included both environmentally plastic (m_p) and fixed (m_f) maternal effects (table S5), the latter being the more important source of variation in clutch size (0.3% vs. 2.7%). Whereas m_p is linked to offspring condition, we have no clear hypothesis as to which mechanism underlies m_f in our population. Nongenetic maternal inheritance has been linked to transgenerational epigenetic effects in several contexts, including parental care and nutritional stress (Champagne 2008; Jablonka and Raz 2009). In mammals, for example, maternal postconception protein restriction and prenatal famine induce DNA methylation corresponding to impaired offspring development, with potential consequences for metabolic phenotypes later in life (Tobi et al. 2014; Holland et al. 2016). Rats receiving little grooming as pups show increased stress response and methylation patterns of genes associated with glucocorticoid stress response, setting the stage for their own maternal grooming behavior as adults (Weaver et al. 2004; Szyf et al. 2005). Such epigenetic mechanisms are likely to reset in every generation (Feng et al. 2010). While this mechanism could theoretically underlie both m_p and m_f in our case, they would be a more likely candidate for m_f as they can be reset in every generation, but more empirical work is needed to elucidate the evolutionary importance of epigenetic inheritance in natural populations (Verhoeven et al. 2016).

We had no indication from our long-term data set that m_f was in any way dependent on the environment, despite a considerable year-to-year variation in clutch size (table S1). Kuijper and Hoyle (2015) have argued that maternal effects are in reality not likely fixed but have the ability to evolve positive or negative signs depending on the stability of the environment. Interestingly, our empirical estimate of m_f (-0.21) is congruent with Hoyle and Ezard's (2012) derived value for m (-0.2) at which mean population fitness is predicted to be maximized given a moderate degree of autocorrelation ($\rho = 0.25$) between the environment of development and selection. Using an intuitive measure of the quality of the environment, that is, population-average fledgling weight (see table S2), we find a significantly positive lag-1 autocorrelation of $\rho = 0.36$ ($P < .05$). Thus, m_f, in our population, is close to what we would expect to evolve in an environment that, although varying from year to year, exhibits a reasonable degree of predictability. Such a negative maternal effect, whatever the underlying mechanism, is expected to evolve as it tends to reduce phenotypic variance and enhance mean fitness in the population (Hoyle and Ezard 2012; Kuijper and Hoyle 2015).

The trait variation explained by the maternal effect found here as well as in previous studies seems to be small to modest (Räsänen and Kruuk 2007; McAdam et al. 2014). This has obvious implications for their potential consequences for evolutionary change but also raises the question as to why maternal effects seem to be generally weak. If we viewed a maternal effect as an adaptive plastic effect to prime offspring optimally for expected environmental conditions, then low predictability of the expected environmental conditions would lead to a reduced or absent maternal effect (Uller 2008), analogous to nontransgenerational plasticity (Gienapp et al. 2014). We may also expect small maternal effects if adjusting them to varying environmental conditions is costly, analogous to the costs of phenotypic plasticity (e.g., DeWitt et al. 1998), but our current understanding of costs of plasticity is still limited (Auld et al. 2010). So, maternal effects may be constrained in the same way as other plastic traits and this may explain their small to modest sizes. Furthermore, for maternal effects to evolve to their optimal values, genetic variation in them is required, but our understanding of the (quantitative) genetics of maternal effects in wild populations is even more limited, partly because the necessary data are scarce (McAdam et al. 2014).

In our model, the effects of m_f and m_p on adaptation were projected over a few hundred generations. Realistically, given the transient nature of our empirical approximations, this is the maximum predictive window across which we can endeavour to make projections. Theoretical models that operate at evolutionary timescales predict that environmental shifts are followed by evolution of the maternal effect itself (Kuijper and Hoyle 2015). To complicate matters further, novel environments may release cryptic genetic variation (Lédon-Rettig et al. 2014) as well as increase residual variances (Rowiński and Rogell 2017), affecting the speed with which adaptation can take place (Wilson et al. 2006; Husby et al. 2011; cf. Wood and Brodie III 2016). These issues, among others, make predicting adaptation at evolutionary timescales (i.e., beyond hundreds of generations) a senseless exercise when the goal

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is to use real parameters, as these very parameters originate from a mere snapshot of the environment.

This brings us to the question of whether we can quantify real evolutionary responses resulting from maternal effects in wild populations. Indeed, several articles have shown the potential evolutionary importance of maternal effects in wild populations (e.g., McAdam and Boutin 2004; Badyaev 2005; Wilson et al. 2005; McFarlane et al. 2015), corroborated by laboratory studies (e.g., Yanagi and Tuda 2010; McGlothlin and Galloway 2013; Munday et al. 2017). Note that the maternal effects addressed in these studies are the type that in some way represent a female quality or investment (identified as variance components; but see McAdam and Boutin 2004) and therefore differ from our estimated m_p or m_f. The studies cited, making use of past or present selection regimes, showed that the population's capacity to evolve at least partly bears on the presence of maternal effects, but none of the studies has endeavored to make predictions about future evolutionary trajectories. A way to overcome this would be to make use of estimates originating from populations undergoing substantial directional selection (Kuijper and Hoyle 2015), preferably in combination with long-term cross-fostering experiments (e.g., Postma et al. 2007), which, to date, are rare (Merilä et al. 2001*b*; Kruuk and Hadfield 2007). The outcome of such long-term studies could serve as input for state-of-the-art models to predict—or hindcast—how a population might evolve in the presence of maternal effects. Combined, these methods may be of use in answering this outstanding question in ecology and evolution.

Our world is changing rapidly, with climate change posing an important threat to populations' persistence (McLaughlin et al. 2002; Thomas et al. 2004). To forecast the viability of populations in the long run, we need to understand the rate at which species can adapt to these novel selection pressures (Visser 2008). We observe apparent evolutionary stasis in several populations (Merilä et al. 2001*b*), possibly due to the importance of non-Mendelian inheritance systems such as maternal effects. These inheritance systems may greatly affect evolutionary dynamics (Räsänen and Kruuk 2007; Danchin et al. 2011); yet to quantify this in wild populations we need long-term observations of populations under sustained directional selection (Kuijper and Hoyle 2015; cf. McGlothlin and Galloway 2013). Theoretical models can aid in understanding how such inheritance mechanisms can act at evolutionary timescales (Cobben and van Oers 2016) when they are rooted in reality. Basing ourselves on real data, we show that the potential for environmentally plastic maternal effects to alter the rate of adaptation is limited even under strong, sustained directional selection. To further our understanding of the adaptive potential of nongenetic inheritance, we therefore strongly encourage a closer link between theoretical and empirical work on maternal effects—for example, through collaboration between research groups with access to real data—to achieve accurate predictions about the evolutionary consequences of maternal effects.

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