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ASSESSING ADAPTIVE PHENOTYPIC PLASTICITY BY MEANS OF CONDITIONAL STRATEGIES FROM EMPIRICAL DATA: THE LATENT ENVIRONMENTAL THRESHOLD MODEL

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Conditional strategies are the most common form of discrete phenotypic plasticity. In a conditional strategy, the phenotype expressed by an organism is determined by the difference between an environmental cue and a threshold, both of which may vary among individuals. The environmental threshold model (ETM) has been proposed as a mean to understand the evolution of conditional strategies, but has been surprisingly seldom applied to empirical studies. A hindrance for the application of the ETM is that often, the proximate cue triggering the phenotypic expression and the individual threshold are not measurable, and can only be assessed using a related observable cue. We describe a new statistical model that can be applied in this common situation. The Latent ETM (LETM) allows for a measurement error in the phenotypic expression of the individual environmental cue and a purely genetically determined threshold. We show that coupling our model with quantitative genetic methods allows an evolutionary approach including an estimation of the heritability of conditional strategies. We evaluate the performance of the LETM with a simulation study and illustrate its utility by applying it to empirical data on the size-dependent smolting process for stream-dwelling Atlantic salmon juveniles.

KEY WORDS: Bayesian modeling, conditional strategies, environmental threshold model, phenotypic plasticity, quantitative genetics.

The ability of organisms to adapt to rapidly changing environmental conditions is becoming of applied importance for understanding how they persist (Gienapp et al. 2008; Reed et al. 2010). Phenotypic plasticity (i.e., the ability of a given genotype to produce variable phenotypes, dependent upon environmental conditions) is the most immediate, and potentially adaptive, response of individuals to environmental change (Ghalambor et al. 2007; Gienapp et al. 2008). Its evolution can accelerate phenotypic evolution, which, in turn, can facilitate persistence in new environment (Lande 2009; Chevin and Lande 2010). It can be maintained (i.e., adaptive phenotypic plasticity) in variable environments when reliable cues allow organisms to match their phenotypes to encountered conditions (Ghalambor et al. 2007; Reed et al. 2010). Anthropogenic disturbances and/or climate change can reduce the reliability of cues as indicators of optimal life-history decisions, rendering previously

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adaptive plastic responses suboptimal in new environmental contexts.

In the case of phenotypic plasticity with discrete traits (e.g., maturation at given age, polymorphism in defensive structures, or alternative mating tactics), the concept of conditional strategies (Gross 1996) has become a popular framework (Roff 2011). Tomkins and Hazel (2007) defined a conditional strategy as a genetically determined decision rule containing a conditional clause. For example, with binary traits, that is, traits with two possible categorical phenotypic states (also known as tactics), the phenotype expressed by an individual may depend on an environmental cue and the choice between phenotypes may result from a physiological "comparison" between the cue and a threshold (or switch point; Oliveira et al. 2008).

Hazel et al. (1990; see also Hazel et al. 2004 and Tomkins and Hazel 2007) developed the environmental threshold model (ETM) for representing a conditional strategy as an environmentally cued threshold trait (Roff 1996). In the ETM, the individual status is determined by the environmental cue, which is compared to the threshold. Thresholds vary among individuals and exhibit additive genetic variance. By incorporating environmental and genetic influences, the ETM encapsulates both phenotypic plasticity and evolutionary change in a unique framework (Tomkins and Hazel 2007). Specifically, changes in the cue distribution directly translate into a change in the phenotype proportions, thereby reflecting phenotypic plasticity. Similarly, evolutionary changes shift the threshold distributions (Hazel et al. 1990) and modify the phenotypic proportions, potentially independently of changes in the distribution of the cue.

Under conditions of sustained directional change, the costs and limits of phenotypic plasticity (DeWitt et al. 1998) require genetic variation in order for populations to continue to adapt to the new conditions by means of natural selection (Pigliucci 2005). With respect to conditional strategies, the ability of the ETM to accommodate both phenotypic plasticity and evolution within a single framework is appealing for assessing the evolution of conditional strategies in the wild (Tomkins and Hazel 2007; Roff 2011). However, for the ETM to be useful in real case studies, its various components (alternative phenotypes, environmental cues, individual genetic effects on the thresholds, and their related distributional parameters) must be quantified. The ETM was initially formalized mathematically (Hazel et al. 1990; Hazel et al. 2004) but statistical tools are needed to draw inferences from empirical data. Here, we make the distinction between "observables" (i.e., those variables that can be directly measured) and "non-observables" (i.e., those variables that can only be inferred, typically the thresholds). Empirical data often produces noisy measures of underlying traits, and it is thus important to account for this uncertainty (or measurement error). We introduce a new statistical modeling framework, which embeds the ETM to make it amenable to proper statistical inference on empirical data.

In the ETM, as the individual thresholds and the parameters of their distribution are conceptual and unknown quantities, they represent non-observable quantities. In contrast, the phenotypes expressed by individuals are observable. Whether the environmental cue is observable is often more complex. The choice of a single and observable environmental feature (e.g., ambient temperature), although logistically tractable, is necessarily to some extent arbitrary as the ways in which organisms perceive their environment is undoubtedly multifactorial (Price and Schluter 1991; Merilä and Sheldon 1999). We follow Dieckmann and Heino (2007) such that "it is more practical to let the organisms themselves do the integration over time and environmental effects." In fish, growth rate and/or size at a given age are known to be strongly influenced by the environment and are thus considered as integrating various environmental factors (Hutchings 2004; Dieckmann and Heino 2007). Rather than considering observable phenotypes as a determinant of the biological process (i.e., size-determining maturation process), we take the alternate approach in assuming that they are a manifestation of an underlying process. We argue that this assumption is biologically more realistic.

Regardless of which way the investigator chooses to measure the environmental cue, be it as an external environmental variable or a biological trait, the proximate mechanism by which the organism assesses its environment will most often remain unknown (Metcalfe 1998; Tufto 2000; Thorpe 2007; Tomkins and Hazel 2007). Therefore, we argue that this source of uncertainty should be explicitly incorporated in a statistical framework to assess conditional strategies by means of the ETM. We propose to split the environmental cue of the ETM into two distinct but related quantities: the *proximate cue* which is to be compared with a threshold that would trigger the phenotype expressed by an individual and an *observable cue* which can be readily measured. Although the proximate cue is unobservable (e.g., underlying physiological mechanisms such as hormones; see Willmore et al. 2007; Aubin-Horth and Renn 2009; McNamara and Houston 2009), it should be correlated with the observable cue (e.g., morphology such as body size or growth; see Fairbairn and Yadlowski 1997). The threshold versus proximate cue comparison is now a fully hidden process as it involves two unobservable variables. This process combines both an environmental effect, through the proximate cue, and a genetic effect, through the threshold. In a modeling context, both aspects need to be distinguished in a model so that they can be interpreted separately. For this reason, we further assume that the threshold is purely genetically determined, in keeping with Roff's (1994) statement that "the critical assumption of the ETM is that there is a single and unique switch point (threshold) for each genotype."

We describe a new statistical model, the Latent ETM (LETM) and highlight its connections with statistical models in quantitative genetics. The LETM structure makes the variation in the additive genetic component of the conditional strategy (the variance of the threshold distribution) relatively easy to estimate. This feature is crucial because the genetic variance of the threshold is a key element for assessing the evolutionary potential of a conditional strategy (Hazel et al. 1990; Hazel et al. 2004; Tomkins and Hazel 2007). In addition, we show that the use of genetic relatedness between individuals is required for the estimation process by separating the threshold genetic variance from random noise in the proximate versus observable cue relationship. Finally, we illustrate our approach with a case study on the size-dependent smolting process for stream-dwelling juvenile Atlantic salmon in the Scorff River (Southern Brittany, France). Overall, the LETM approach can be fruitfully applied whenever the conditional strategy framework is relevant, pending the availability of individual data for at least the alternative phenotypes involved and a related observable cue.

The Latent Environmental Threshold Model

We use the notation $A|B \sim Dist(f(B))$ to denote a set of random variables A distributed conditionally on the set of variables B according to a probability distribution $Dist$ with parameters that are a function f of B. Observable quantities are denoted with capital Roman letters and unknowns with Greek letters.

FROM THE ETM TO THE LETM

For an individual i, the threshold modeling framework stipulates that if the value of a cue η_i is larger (respectively lower) than a threshold θ_i, then it triggers the expression of a phenotype, say migrant (respectively resident). If Y_i is the binary variable indicator of the phenotype (e.g., 1 for migrant and 0 for resident), then we have:

$$Y_i = \left\{ \begin{array}{l} 1 \text{ if } \eta_i \geq \theta_i \\ 0 \text{ if } \eta_i < \theta_i \end{array} \right\}. \quad (1)$$

The cue η_i varies among individuals as a function of the environment, whereas the threshold θ_i is considered an intrinsic property of the individuals, independent of η_i. The threshold θ_i also varies among individuals and is a polygenic quantitative trait that is normally distributed with mean μ_θ and standard deviation σ_θ, as typically assumed in quantitative genetics (Hazel et al. 1990; Lynch and Walsh 1998; Tomkins and Hazel 2007):

$$\theta_i \mid \mu_\theta, \sigma_\theta \sim N(\mu_\theta, \sigma_\theta). \quad (2)$$

Equations (1) and (2) and their associated assumptions correspond exactly to the ETM (Hazel et al. 1990). Equation (1) represents the putative proximate mechanism explaining the phenotypic expression. In this mechanism, the phenotype Y_i is observable, whereas the threshold θ_i is not; it is a conceptual variable referred to as a latent variable in statistical terminology (Congdon 2007).

We introduce two additional assumptions in the specification of the LETM. First, we assume that the proximate cue η_i is unobservable. By doing so, we explicitly recognize that often little biological knowledge is available regarding the proximate mechanism influencing the expression of the phenotype (Metcalfe 1998; Thorpe 2007; Tomkins and Hazel 2007). Although η_i is not observable, an observable proxy X_i can be measured which is correlated with η_i. The distribution of the unknown proximate cue η_i can be expressed conditionally on the observable proxy X_i with some residual error ε_i:

$$\eta_i = F(X_i) + \varepsilon_i, \quad (3)$$

where F is a function, for example, a linear relationship, summarizing the link between the proximate and the observable cue. The residual error ε_i is assumed normally distributed with mean 0 and standard deviation σ_η:

$$\varepsilon_i \sim N(0, \sigma_\eta). \quad (4)$$

Note that equations (3) and (4) correspond to the Berkson measurement error model in the statistical literature (Congdon 2007). This formulation has the advantage of being assumption free regarding the distribution of the X_i. Consequently, the statistical analysis is made more flexible as it is independent of the procedure used for collecting the X_i observations. They can come either from field sampling or from controlled experiments.

The second assumption is in line with Roff's (1994) statement that there may be a unique threshold for each genotype. Specifically, we consider the threshold θ_i as being completely genetically determined which implies that the standard deviation σ_θ in equation (2) is a measure of genetic variability. This was also proposed by Hazel et al. (1990) to show the effect of the selection on the threshold distribution. By doing so, the various components involved in the model are clearly distinguished, hence making the inference process easier: the environment, the proximate mechanisms triggering the phenotype expression (conditionally on the environment), and the genetic control on this mechanism.

The statistical model defined by equations (1)–(4) considers the ETM as a latent structure connecting the observed environment with the observed phenotypes. We, therefore, refer to it as the LETM. The conditional structure of the LETM can be summarized by a directed acyclic graph (Fig. 1).

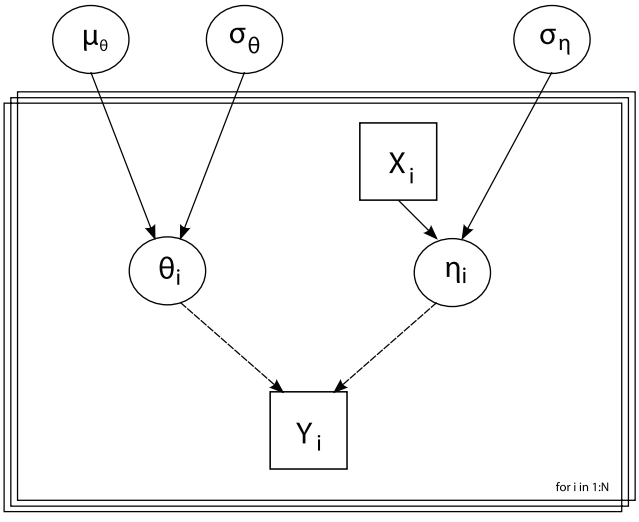

Figure 1. Directed acyclic graph of the latent environmental threshold model. Squares represent observable data and circles represent unknown quantities to be estimated. For an individual *i*, the threshold θ_i is normally distributed with mean μ_θ and standard deviation σ_θ. The proximate cue η_i is normally distributed with a mean of the observable cue X_i and standard deviation σ_η. Finally, Y_i is a binary indicator variable of the observed phenotype and is modeled as a function of the threshold and the proximate cue at the individual level, with $Y_i = 1$ when $\theta_i < \eta_i$. Solid and broken arrows represent stochastic and logical dependence, respectively. The model is fit to observations of phenotyped individuals, hence the boxes denoting a loop over $i = 1, 2, \ldots, N$ individuals.

ALTERNATIVE FORMULATION OF THE LETM

Equation (1) can be reformulated as:

$$Y_i = \left\{ \begin{array}{l} 1 \text{ if } z_i \geq 0 \\ 0 \text{ if } z_i < 0 \end{array} \right\}, \quad (5)$$

where z_i is the difference (η_i - θ_i) between the proximate cue and the individual threshold. Taking the proximate versus observable distinction into account (eq. 3), z_i is given by:

$$z_i = X_i - \theta_i + \varepsilon_i, \quad (6)$$

where ε_i and θ_i, are independent and normally distributed (eqs. 2 and 4), hence z_i is normally distributed with mean ($X_i - \mu_\theta$) and variance $\sigma_P^2 = \sigma_\theta^2 + \sigma_\eta^2$.

From equations (5) and (6), the LETM can be seen as a threshold model often used in quantitative genetics to model binary traits (Falconer 1981; Gianola 1982; Sorensen et al. 1995). In a threshold model, Y_i is distributed as a Bernoulli distribution with probability p_i, where

$$p_i = \Pr(Y_i = 1) = \Pr(z_i \geq 0) = \Phi\left(\frac{X_i - \mu_\theta}{\sqrt{\sigma_\theta^2 + \sigma_\eta^2}}\right), \quad (7)$$

where ϕ is the cumulative distribution function of a standardized normal distribution.

In this framework, z_i is a latent variable often called a liability. Equation (6) is analogous to a standard "animal model" (Kruuk 2004; Wilson et al. 2010) and splits z_i into three terms: X_i the observed cue is a fixed effect, θ_i the threshold is a random additive genetic effect (also called the genetic value or the breeding value for individual *i*), and ε_i is a residual error term. In the animal model, σ_P^2 is the total phenotypic variance and the ratio of the additive genetic variance (σ_θ^2) to the total phenotypic variance (σ_P^2) is the heritability (h^2) of the latent trait z_i. It is also considered as the heritability of the associated conditional strategy (Lynch and Walsh 1998).

IDENTIFIABILITY ISSUES

The animal model is known to be prone to identifiability issues (i.e., difficulty in distinguishing variance components in the estimation process) as it combines several unobservable random effects (Kruuk 2004; Wilson et al. 2010). Regarding the LETM, the issue lies in the separation of the genetic effects represented by the threshold θ_i from the residual error term ε_i. When data are available only for the observable cue X_i and the alternative phenotypes Y_i, there is potential confusion between the genetic variance σ_θ^2 and the residual error variance σ_η^2. As a consequence, only the total phenotypic variance (σ_P^2) is identifiable, whereas the proportion of total variance explained by the variability in the threshold—that is, the heritability $h^2 = \sigma_\theta^2/\sigma_P^2$—is not. To circumvent this issue, additional information is required. To make the animal model identifiable, pedigree data on individual relatedness are used and the individual phenotypes are considered as nonindependent because related individuals share genes. More specifically, the individual additive genetic effects covary and the structure of the covariance matrix depends on the relatedness between individuals. In the case of the LETM, we assume that the individual thresholds θ_i covary according to the individual relatedness, equation (2) therefore becomes:

$$\theta_i \mid \mu_\theta, \sigma_\theta^2, A \sim \text{MVN}(\mu_\theta, G), \quad (8)$$

where MVN is the multivariate normal distribution, θ is the vector of thresholds (i.e. additive genetic effects), and G is the variance–covariance genetic matrix. The matrix G is given by $G = A \times \sigma_\theta^2$, where A is the additive genetic relationship matrix and σ_θ^2 is the additive genetic variance. The additive genetic relationship matrix A contains all the pairwise values of relatedness (two times the coefficient of coancestry, i.e., 0.5 for parent–offspring pairs and full siblings, 0.25 for half siblings, and 0.125 for first cousins; see Wilson et al. 2010 for more details).

BAYESIAN STATISTICAL INFERENCE

Bayesian approaches using Markov chain Monte Carlo (MCMC) algorithms provide a flexible framework for analyzing latent variables models and their conditional structure (Clark 2004). We therefore adopted this approach to fit the LETM to data. Specifically, the Bayesian approach combines the likelihood (i.e., information derived from the observed data) and the prior distribution of the unknown quantities (i.e., knowledge available before the data were observed) to produce a joint probability distribution of all model unknowns, conditionally on the observed data (the so-called joint posterior distribution; see Gelman et al. 2004; Ellison 2004 and McCarthy 2007; for more details about the Bayesian statistical modeling). If the (noninformative) prior and the posterior distributions of a given parameter largely overlap, then there is not enough information in the data to estimate this parameter. The joint posterior distributions of all the model unknowns, that is, the parameters (μ_θ, σ^2_θ, σ^2_η), the individual thresholds, and the proximate cues (θ_i, η_i), were obtained by means of MCMC sampling as implemented in the OpenBUGS software (Lunn et al. 2009). The code of the LETM as well as an example of data are available at (http://www.cefe.cnrs.fr/biom/zips/LETM.txt). We ran two parallel MCMC chains and retained 25,000 iterations after an initial burn-in of 5000 iterations. Convergence of MCMC sampling was assessed by means of the Brooks-Gelman-Rubin diagnostic (Brooks and Gelman 1998).

A Bayesian analysis requires specifying prior probability distributions for the model parameters, that is, the unknown quantities that are not conditioned by any other quantity in the model (μ_θ, σ_θ, σ_η; Fig. 1). In our study, all priors were noninformative or weakly informative (e.g., priors on threshold and proximate cue variance). The prior on the mean of the threshold distribution μ_θ was specified as a normal distribution with mean 0 and a large variance (1000). To make the assessment of identifiability issues easier, priors on the standard deviations σ_θ and σ_η were not defined directly but rather on the total phenotypic variance and the heritability h^2. Note that because there is a one-to-one transformation relating (σ^2_P, h^2) to (σ^2_θ, σ^2_η), assigning a prior to (σ^2_P, h^2) induces a prior on (σ^2_θ, σ^2_η) as well (Gelman et al. 2004). We used a uniform distribution between 0 and a large value (100) for σ_P as recommended by Gelman (2006) and a uniform distribution between 0 and 1 for h^2.

Simulation Study

We evaluated the performance of the LETM for statistical inference, with simulated data. The simulation model was the LETM itself with known parameter values and including three common genetic structures for the θ_i's, that is, full siblings, half siblings, and a mixture of both. The covariation in the θ_i's according to their relatedness (eq. 8) was explicitly included in the simulation model. Note that clonal genetic structure can be used (coefficient of relatedness equal to 1; see Ostrowski et al. 2000 for an illustration of such an experimental protocol) but we believe our approach is more realistic regarding data at hand for ecologists and evolutionists. Statistical inference was then derived from the simulated data to check whether the LETM provided accurate estimates of the parameters (μ_θ, σ^2_θ, σ^2_η) and of the individual latent variables (the thresholds θ_i and proximate cues η_i). Genetic information regarding the θ_i's was incorporated in the fitting process.

We generated 20 datasets consisting of 400 individuals and structured as 20 batches of 20 individuals. Within each batch individuals were either full sibling, half sibling, or a mixture of both, whereas between batch, individuals were unrelated. First, the threshold values were generated from the multivariate normal distribution with mean $\mu_\theta = 0$ and a genetic variance–covariance matrix G. The matrix G is the product of an additive genetic relationship matrix A and genetic variance (eqs. 2 and 8). The additive genetic relationship matrix A was generated according to each of the three designs: (1) with values of relatedness of 0.5 between individuals within a batch in the case of the "full sibling design," (2) 0.25 for the "half sibling design," and (3) a mixture of both in the "mixture design." In the latter case, we simulated a pedigree for each batch from the R package "GeneticsPed" (Bioconductor). First, we sampled the number of potential breeders in a Poisson distribution with parameter set to 2 for both sexes (i.e., generating two potential breeders on average for each sex). GeneticsPed generated pedigree from potential breeders allowing the reconstruction of kin groups (mixtures of full siblings and half siblings and sometimes higher degrees of relatedness such as cousins if required) and the associated additive genetic relationship matrix A. The threshold (i.e., genetic) variance was fixed to 0.5. Second, we generated an observed cue X_i value for each individual i from a normal distribution with mean 0 and standard deviation 1. For each individual i, given the value of the observed cue X_i, we generated its proximate cue η_i from a normal distribution with mean X_i and variance $\sigma^2_\eta = 0.5$ (eq. 3). Thus, the "actual" total phenotypic variance is 1 and the "actual" heritability of the conditional strategy is 0.5 in the data simulation model. Finally, given the values of the proximate cue η_i and that of the threshold θ_i, we assigned the phenotype indicator values Y_i (eq. 1). Note that simulated data are more variable in the proximate cue than in their threshold, as it should often be the case with real data (Tomkins and Hazel 2007).

Application to Alternative Life-History Tactics in the Atlantic Salmon

The Atlantic salmon is an anadromous species that occupies both freshwater and the ocean during its life cycle (Verspoor et al.

2007). In Brittany, the juvenile phase in freshwater lasts one or two years (Baglinière et al. 1993). Thereafter, fish migrate to the ocean and return after one or two years to their native stream to breed. Atlantic salmon are conditional strategists with state-dependent choice among alternative life-history tactics (Hutchings and Myers 1994; Gross 1996; Thorpe et al. 1998; Garant et al. 2003; Hutchings 2004; Hutchings 2011). During their first year of life in their natal river, young of the year (YOY; i.e., individuals less than one year old) can either migrate to the ocean the next spring or reside in freshwater for an additional year (Thorpe et al. 1998). The choice between the migrant versus the resident alternative tactics (i.e., phenotypes) is related to the size of the individuals in their first autumn (Nicieza et al. 1991; Thorpe et al. 1998; Thorpe and Metcalfe 1998).

Although size is an observable cue, it is probably best considered as a proxy for energetic status (Thorpe et al. 1998), that is, likely a more proximate cue, which is to be compared to a threshold for triggering seaward migration the next spring (Thorpe et al. 1998; Mangel and Satterthwaite 2008; Satterthwaite et al. 2010). The individual energetic status influences this life-history choice (Jonsson and Jonsson 2005) because migration to the ocean is preceded by the smolting process, which is an energetically costly process of preparing individuals for seawater life (McCormick and Hansen 1998; Thorpe et al. 1998). The energetic status reflects the way that energy is acquired, stored, and used; and is strongly influenced by the environmental conditions experienced by each individual (e.g., food availability, temperature regime, or density of conspecifics; Elliott and Hurley 1997; Forseth et al. 2001; Jones et al. 2002; Imre et al. 2005; Murphy et al. 2006; Finstad et al. 2010). Under the LETM, we consider migrant versus resident (at one year of age) as alternative phenotypes and size in autumn of YOYs as an observable cue indicative of the individual energetic status (i.e., the proximate cue triggering phenotype expression).

DATA COLLECTION

In autumn 2006, YOY juveniles were sampled by electrofishing at 39 stations along the main course of the Scorff. Every fish captured was measured (fork length, to the nearest 1 mm) and individually marked with a passive integrative transponder (PIT) tag (11 mm long, 2.2 mm in diameter) inserted into the peritoneal cavity according to the protocol described in Acolas et al. (2007). One-year old seaward migrating juveniles (smolts) previously PIT tagged were identified during their downstream migration in the spring of 2007. They were captured at two successive traps located at the lower end of the river system below all sites in which YOY were marked. At both facilities, their individual PIT tags were identified. Eventually, PIT-tagged anadromous salmon were recaptured in 2008 and 2009 when returning into the Scorff river after one or two years at sea. They were sampled at the Princes Mill facility in a trap designed to catch upstream migrating adults. PIT tagged resident juveniles, that is, future two years old smolts, were identified in autumn 2008 using sampling by electrofishing according to same protocol used for the YOY the previous year. Two-year old smolts were also recaptured the following spring (2009) and identified by their PIT tags.

Here, we considered the set of YOY juveniles marked in autumn 2006 and recaptured later on ($n = 104$). For each of them, we recorded both its phenotype (migrant vs. resident) and its observable cue (fork length at first autumn).

MODELING

For each individual i, the proximate cue η_i (energetic status) was assumed to be normally distributed with the mean of its fork length at first autumn Fl_i (the observable cue) and standard deviation σ_η (eq. 3). The alternative phenotype indicator Y_i (eq. 1) takes the value 1 if individual i migrates to sea at one year of age, and 0 if it stays an additional year in fresh water.

As YOY juveniles tend to stay close to their natal spawning nest (Beall et al. 1994; Einum et al. 2008; Foldvik et al. 2010), we assumed that YOY captured in the same station in autumn could be all brothers and sisters (i.e., full-siblings' genetic structure) or half brothers and half sisters (i.e., half-siblings' genetic structure) or, a mixture of both (i.e., mixtures' genetic structure). These assumptions were made to illustrate the greater genetic similarity of YOY salmon within, than between, sites. The mixture design is probably the most realistic option because of complex mating patterns in Atlantic salmon with both sexes having several partners (Thériault et al. 2007). In the mixture design, we assumed that the number of potential breeders was low at each sampling stations and that males outnumbered females (Jordan and Youngson 1992; Grimardias et al. 2010). As the pedigree of the fish sampled is unknown, we generated 20 mixtures' genetic structure (i.e., additive genetic relationship matrix A) according to the same protocol as in the simulation study (see "Simulation study" section above) with each station corresponding to a batch made of a mixture of full siblings, half siblings (and first cousins if required).

Results

SIMULATION STUDY

Whatever the genetic structure considered, the comparison of posterior and prior distributions showed that the information contained in the data led to considerable updating of the prior distributions. The LETM properly estimated the threshold mean μ_θ and the total phenotypic variance; the posterior medians of these parameters were close to their true value (Fig. 2). The posterior distributions of σ^2_θ and σ^2_η were well estimated too indicating that these parameters were identifiable. The heritability h^2

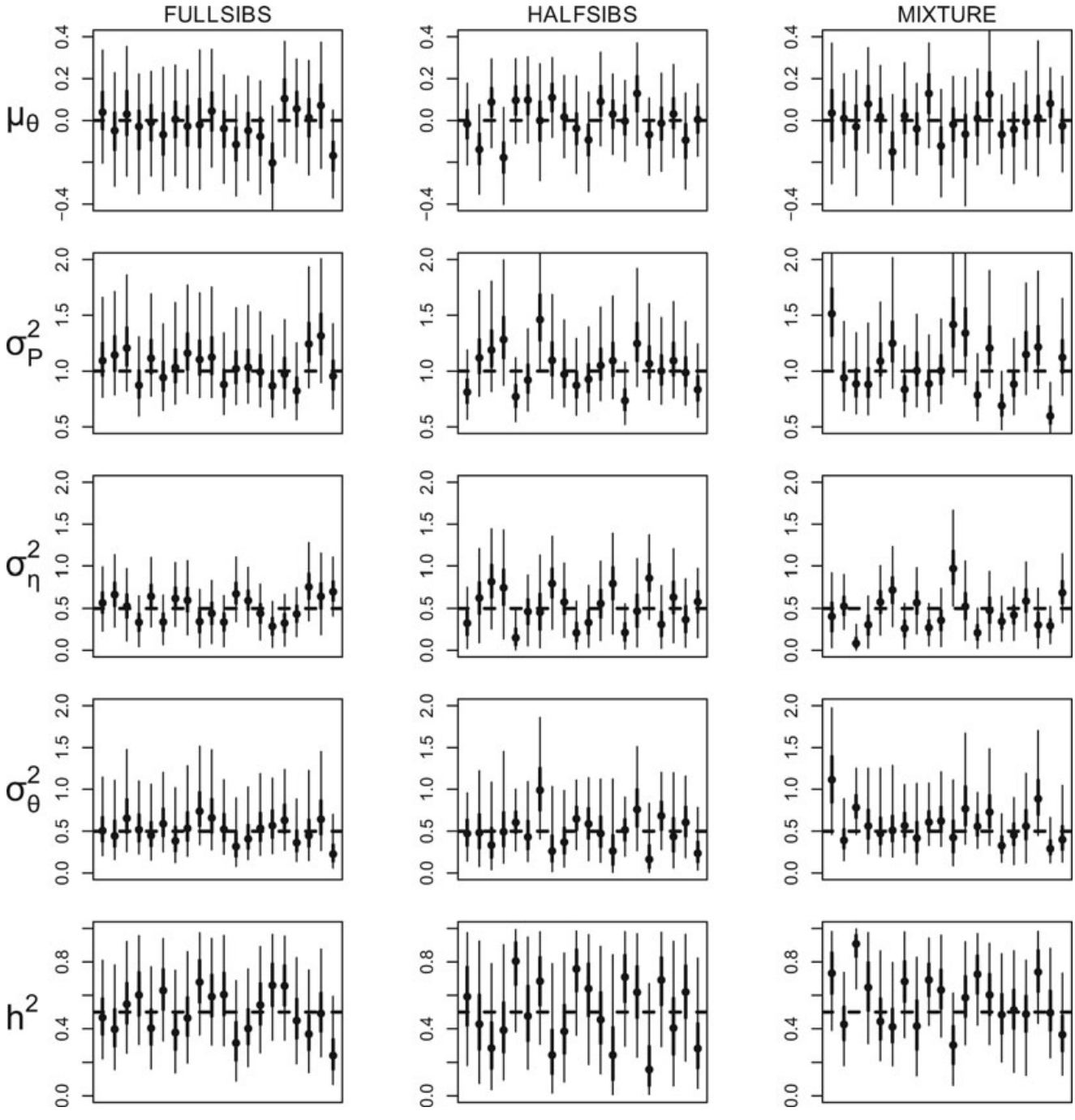

Figure 2. Posterior distributions of the latent environmental threshold model parameters for each genetic structure (full siblings, half siblings, and mixture) and for 20 replicate datasets. The median (black point) and the 95% posterior probability interval (solid lines) are displayed based on 25,000 Markov chain Monte Carlo samples. The actual values are also displayed (dashed lines).

could therefore be estimated: its posterior distribution was much narrower than its prior and the actual value was very close to the posterior median (Fig. 2). In fullsibs design, uncertainty was smaller than in halfsibs design confirming that the power to infer from half-sibling families is less than from full-sibling families (Roff 1997). Uncertainty in the mixture design was intermediate.

At the individual level, the proximate cue η_i and the threshold θ_i were estimated without systematic bias and the actual simulated values fell in most instances within the 95% posterior probability interval (PPI, also called credible interval, which is defined as the interval between the 2.5 and 97.5 percentiles of the posterior distribution; Fig. 3).

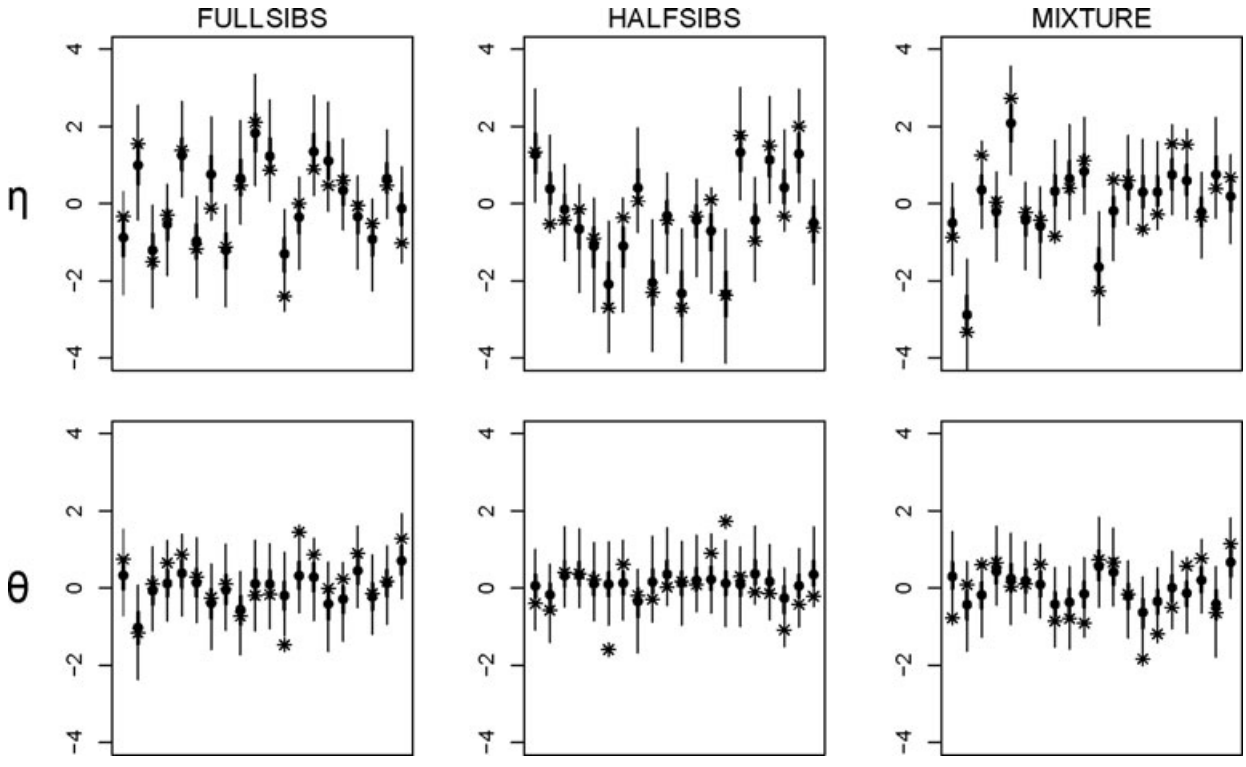

Figure 3. Posterior distributions of proximate cue η_i and threshold θ_i for the latent environmental threshold model for one randomly chosen individual in each of the 20 batches of 1 (out of 20) replicate datasets. The median (black point) and the 95% and 50% posterior probability interval (solid lines and bold lines, respectively) are displayed based on 25,000 Markov chain Monte Carlo samples. The actual values are also displayed (stars).

CASE STUDY

Using the LETM framework, we were able to obtain precise estimates of the mean latent threshold μ_θ and the total phenotypic variance whatever the genetic structure considered (Fig. 4). The posterior distribution of the heritability h^2 showed the information contained in the data led to substantial updating of the prior distribution, indicating that σ^2_θ and σ^2_η could be identified. h^2 posterior distribution favors a high heritability value with a posterior mean of approximately 0.77. In agreement with the simulation study, results were very similar between genetic designs. In fullsibs design, uncertainty was smaller than in halfsibs design whereas mixture design was intermediate depending on proportions of fullsibs and halfsibs.

Estimates of the proximate cue and of the threshold at the individual level were also obtained (Fig. 5). Again, results were very similar between genetic designs. YOY salmon appeared much more variable in the proximate cue than in their threshold. The proximate cue is a conceptual quantity and, as such, its scale is arbitrary. Here, given the measurement error structure of the LETM (eq. 3), its scale is the same as that of the observed cue. For example, a proximate cue 90 can be interpreted as the mean energetic status of a YOY with a 90-mm-long fork in autumn. For the same reason, the mean threshold μ_θ can be either interpreted as the energetic status (proximate cue; eq. 5) or the fork length in autumn (observed cue; eq. 6) of a YOY salmon having an equal probability of becoming migrant or resident.

Discussion

Conditional strategies are the most common form of discrete phenotypic plasticity within species (Gross 1996). Understanding how plasticity, in general, and these strategies, specifically, evolve and are maintained by natural selection is crucial for our understanding of phenotypic and life-history evolution (Pigliucci 2005). The ETM accounts for both genetic variation and environmental cues that affect phenotypic expression. For this reason, in their review of the theoretical models that have been proposed to understand the evolution of phenotypic plasticity in the conditional strategy framework, Tomkins and Hazel (2007) argued that the ETM is "the best model available currently for understanding the evolution and maintenance of conditional strategies." Nonetheless, the ETM has rarely been applied to the study of adaptive phenotypic plasticity both in the wild (Edeline 2007 refers to it but in a rather qualitative way) and under

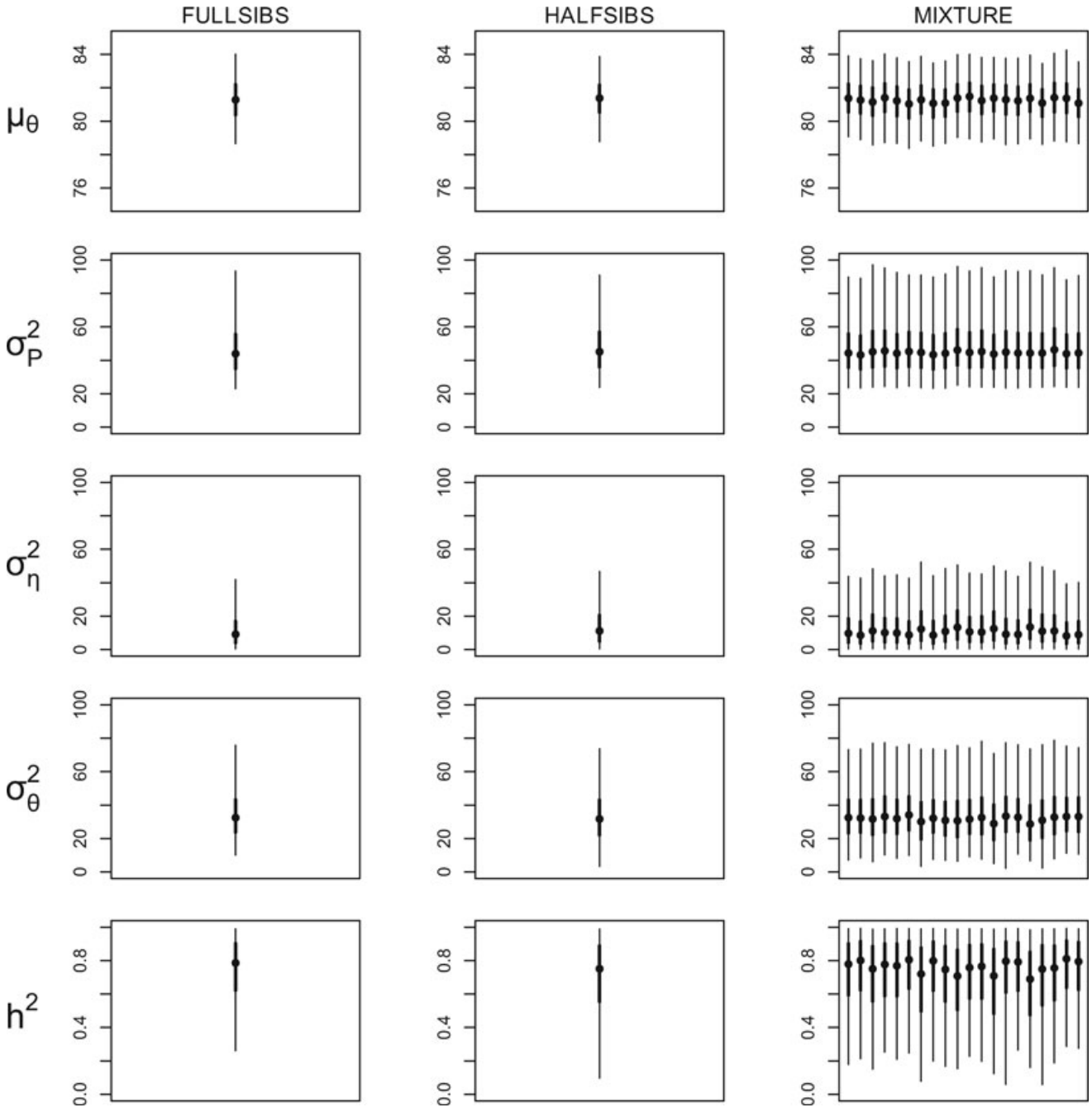

Figure 4. Posterior distributions of the latent environmental threshold model parameters for Atlantic salmon data from the Scorff. Parameters for each genetic structure, that is, full siblings, half siblings, and mixture is shown. For the later, 20 putative mixtures are represented. The median (black point) and the 95% and 50% posterior probability interval (solid lines and bold lines, respectively) are displayed.

controlled experimental conditions (Ostrowski et al. 2000). We believe this is because the ETM was not conceived as a statistical tool to deal with observed data. Here, we developed a statistical model, the LETM that includes the ETM as its core theoretical process.

Several methods exist to estimate heritability (see Roff 1997 for a review). However, most of them are not appropriate for assessing heritability of conditional strategies with empirical data, especially when collected in the wild. Indeed, they have been developed to analyze data obtained in controlled/laboratory conditions involving no environmental variations and perfect knowledge of the pedigree, including sometimes parents' phenotype. Our approach does not suffer from these restrictions and can be applied with only relatedness data although the parents of the observed individuals are unknown. The "Fullsibs'method" (i.e., an analysis of variance based approach) is the only classical method

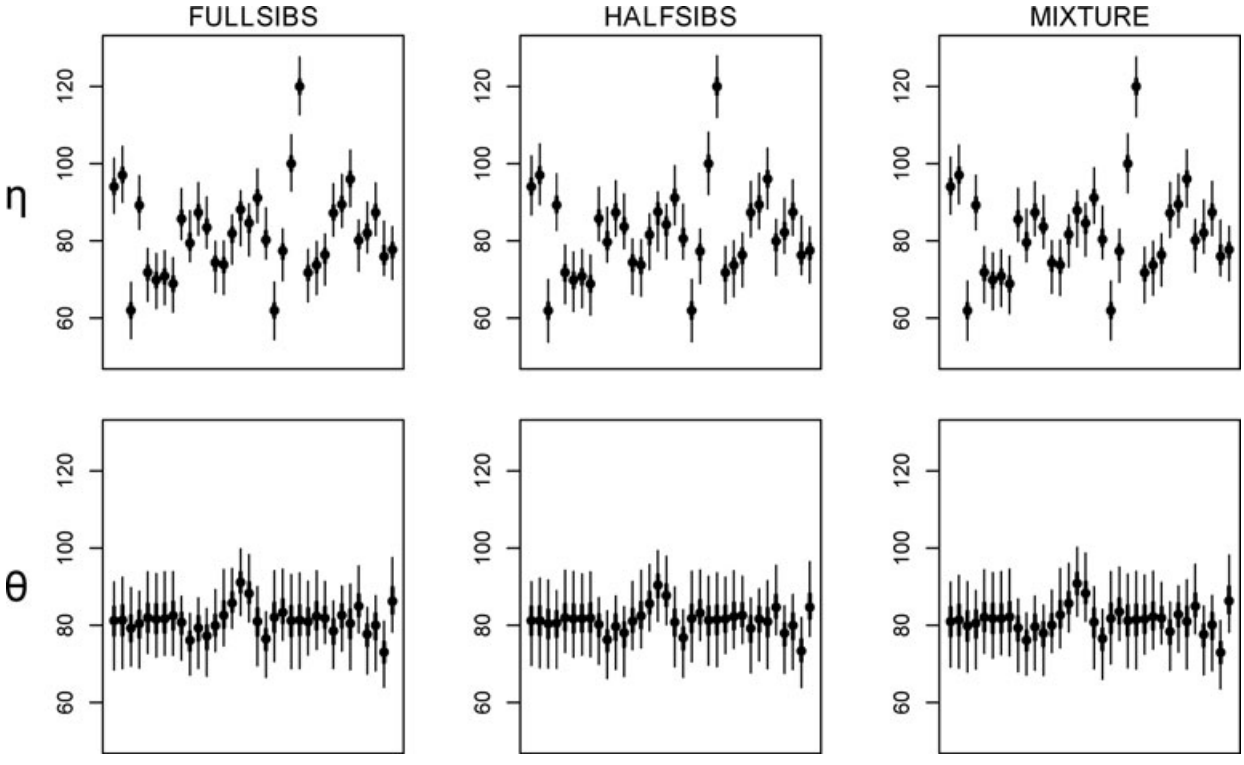

Figure 5. Posterior distributions of proximate cue η_i and threshold θ_i for the latent environmental threshold model for one individual randomly picked in each station along the main course of the Scorff and for each genetic structure, full siblings, half siblings, and mixture. For the later, one mixture was randomly picked out of the 20 putative mixtures. The median (black point) and the 95% and 50% posterior probability interval (solid lines and bold lines, respectively) are displayed.

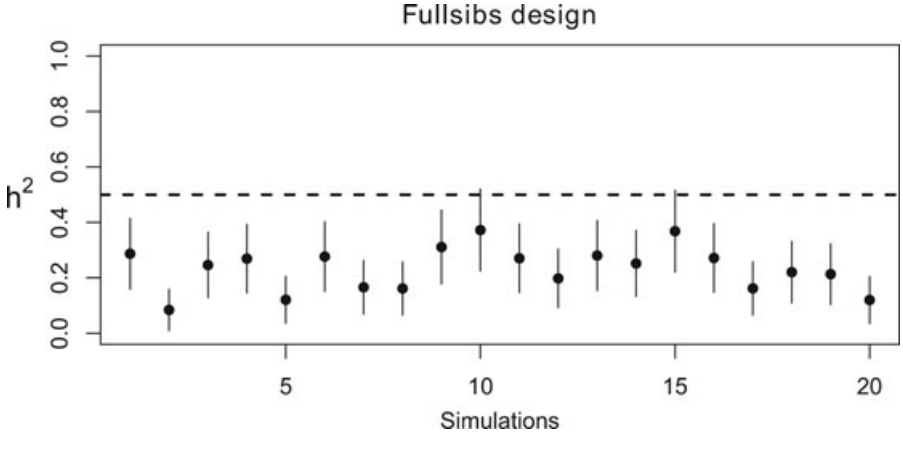

Figure 6. Mean and standard deviation of the heritability estimates calculated using the classical "Fullsibs methods" (see Roff 1997) for the 20 replicated datasets used to test the latent environmental threshold model. The actual value is also displayed (dashed lines).

listed in Roff (1997) that can be applied to our data. We used it (see usual formulas in Roff, 1997) to analyze our simulated datasets (fullsibs design). In contrast with our LETM, this method systematically underestimates heritability of conditional strategies (Fig. 6).

The originality of our approach lies in the observable versus proximate cue distinction, with the latter being unobservable but effectively triggering the phenotypic expression. As a consequence, the ETM becomes a fully embedded process within the LETM, linking the observable environment to the observable phenotype. We take advantage of this feature to explicitly separate the genetic component from the environmental component involved in a conditional strategy. The LETM allows the estimation not only of the parameters of the threshold

distribution, but also of the proximate cue and the threshold at the individual level. As the LETM is a statistical model inspired by quantitative genetics, individual relatedness data can be used to circumvent the identifiability issue affecting the heritability of the conditional strategy. The accuracy of the genetic threshold variance estimates, a key parameter for assessing the evolutionary potential of a conditional strategy (Tomkins and Hazel 2007), is subsequently improved. When data are only available for the alternative phenotypes and the observable cue, the LETM is not fully identifiable.

The proposed distinction between observable and (unobservable) proximate cues is supported by Ostrowski et al.'s (2000) study on the snail *Bultinus truncatus*. They tested the ETM in a set of experiments in which both the genotype and the environment were controlled. In contrast with what was expected under the ETM, they observed significant random variation in the phenotypic expression for any environment × genotype combination they used. They hypothesized that microenvironmental, uncontrolled variation in the threshold explained this residual random variation. We contend the proximate versus observable cue dichotomy is a more sensible alternative hypothesis. In the case of Ostrowski et al. (2000)'s study, it would mean that the organisms assess temperature—the observable environmental cue that is experimentally controlled—through an unknown proximate mechanism with some random "measurement error." The proximate cue would then only be correlated with temperature.

Despite the introduction of the proximate versus observable cue distinction, the LETM is still a relatively simple model in the version we presented here. This transpires from its formulation as specific case of an animal model (eq. 6; see Kruuk 2004; Kruuk and Hill 2008; Wilson et al. 2010). Building upon the LETM outlined here to incorporate more complex structures could allow further improvements in parameter estimation. When biological traits are used as an observable environmental cue, the latter can have a genetic component (Gienapp and Merilä 2010), which could be correlated to the genetic threshold. For example, in salmonids, fish size is considered as an observable environmental cue, but it has also a genetic basis and is heritable (Garant et al. 2003; Thériault et al. 2007; Carlson and Seamons 2008; Serbezov et al. 2010; Varian and Nichols 2010). There is no theoretical reason to restrain the complexity of the animal model within the LETM framework for improving its biological realism. The statistical ecologist working with empirical data, however, might be constrained by identifiability issues, given the information available in the data in hand. This is especially true for the LETM due to its threshold structure. Indeed, for the variable z_i (eq. 6), we have only censored information through the observation of the phenotype (i.e., z_i is positive or negative, eq. 5) and not an exact measurement as is usual when the quantitative trait is readily observable. This difficulty is illustrated in the simulation experiment and the salmon case study. With a large number of simulated individuals, reasonably precise heritability estimates could be obtained, indicating that the model was identifiable. In contrast, less precise estimates of heritability were obtained from our case study data (posterior mean $h^2 = 0.77$, SD $= 0.18$ for fullsibs design), which was based on a much smaller number of individuals ($n = 104$) suggesting identifiability issues. Using an experimental setting of common rearing of half-sibling families (866 individuals), Páez et al. (2010) had also low precision in heritability estimates for a binary "propensity to migrate" in Atlantic salmon ($h^2 = 0.77$, SD $= 0.33$). Similar results were obtained from a simulation with 20 groups each made of five brothers and sisters with heritability fixed to 0.8 (results not shown). The presence of additive genetic variance suggests that life-history tactic for migration can respond to selection, whether natural and/or human induced, through evolution of the threshold (Hutchings 2011; Páez et al. 2010). At the same time, in our case study the additive genetic variance of the threshold (σ^2_θ) is low compared to the total variance of the proximate cue, that is, the sum of the empirical variance of the observed cue ($\sigma^2_X = 168.7$) and σ^2_η. This is consistent with the conditional strategy framework for phenotypic plasticity, which implies the adoption of a tactic (i.e., a phenotype) is primarily due to environmental influence.

Although many theoretical approaches have been proposed for studying evolution of phenotypic plasticity and its consequences on adaptation and persistence capacities of population (see Lande 2009; Reed et al. 2010), there is still a paucity of ecological empirical studies assessing the evolution of phenotypic plasticity in the wild (Nussey 2005; Nussey et al. 2007; Charmantier et al. 2008), and more particularly of conditional strategies (but see Ostrowski et al. 2000 under controlled conditions; Piché et al. 2008 and Páez et al. 2010). The LETM opens up interesting prospects for the study of phenotypic plasticity using observational data. It is a generic tool that could be applied to a wide range of taxa and to different forms of conditional strategies, for example, the induction of defenses against predators (Hammill and Rogers 2008), polyphenic traits in insects (Moczek 2010; Tomkins and Moczek 2009), filial cannibalism (Takeyama et al. 2006), and alternative reproductive tactics (Gross 1996; Piché et al. 2008; Pitnick et al. 2009). By incorporating cues that allow organisms to match their phenotypes to the conditions encountered, it improves our ability to predict how populations will respond to environmental changes (Reed et al. 2010). It also facilitates the quantification of patterns of quantitative genetic variation and heritability of conditional strategies. Although fullsiblingship and/or half-siblings genetic structure was assumed both in our simulated data and in our illustrative salmon case study, the LETM can be applied to any other pedigree structure,

keeping in mind that "the power of a quantitative genetic analysis (also) depends crucially on the pedigree structure" (i.e., its connectedness; Wilson et al. 2010).

In the context of rapid and global environmental change, both evolution and plasticity are likely to prove critical for species adaptation (Gienapp et al. 2008). The joint appraisal of both phenomena from observational data is required, for which the use and further developments of the LETM should help.

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