Genetic basis of between- and within-individual variance of docility

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Key words

heritability, quantitative genetic, behaviour, personality, dhglm

Contribution

D.T.B. led the long-term study. M.P., D.T.B. and J.G.A.M. collected data. J.G.A.M. conceived the ideas for the paper and its structure. J.G.A.M. and E.P. designed and conducted the analyses. J.G.A.M. wrote the manuscript. All authors discussed the results and edited the manuscript.

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Abstract

₂ FiXme: 150 words max for Ecology Letters. add a conclusion

Within a population, phenotypes vary between and within individuals for labile traits expressed repeatedly. However, ecologists have mainly focused on estimating between-individual mean trait variance and neglected variation in within-individual variance. The recent development of double hierarchical models allows concurrent estimation of between-individual differences in both the mean and the within-individual variance of the trait, while correcting for environmental effects. Using long-term data on yellow-bellied marmots, we estimated additive genetic and permanent environment variances in both mean docility and within-individual variance in docility. We found that individuals differed not only in their mean docility, but also in their within-individual variance. In addition, we found an additive genetic basis and a positive genetic covariance between the mean trait and within-individual variation. We demonstrate the evolutionary importance of considering variation in within-individual variance in traits, since the additive genetic basis and genetic correlation with the mean trait can influence the evolutionary trajectory of docility.

INTRODUCTION

2 Phenotypic variance is a central concept of ecology and evolution (Roff 2002). Phenotypic

traits vary among species, among populations, among individuals within populations and, for

4 traits with repeated measures, also within an individual (Roff 2002). Until recently,

within-individual variance has been mainly consider to be either due to plasticity and explained

6 by differences in environmental condition (Pigliucci 2005; Nussey *et al.* 2007) or due to

measurement error (Pigliucci 2005; Westneat *et al.* 2015). Studies of between individual

8 variation focused mainly on differences in the mean value of a trait and considered that within

individual variance is similar across individuals. Indeed, the main assumption of mixed-effects

10 models, a statistical analysis widely used to estimate between-individual variance, is that the

residual variance is identical across individuals (Pinheiro & Bates 2000; Dingemanse &

12 Dochtermann 2013).

In trait repeatedly measured in the same environment, variation in within-individual

14 variance could however be adaptive (Westneat *et al.* 2015; Hill & Mulder 2010). The between

individual variation in within-individual variance is being integrated in evolutionary ecology

16 (Mulder *et al.* 2007; Nussey *et al.* 2007) but its study is still at its premise. Studies in animal

breeding, using a quantitative genetic approach, have estimated the additive genetic basis or

18 within-genotype variance for multiple productivity related traits such as litter size or body

weight (Hill & Mulder 2010; Sae-Lim *et al.* 2015). The exact evolutionary implications of the

20 genetic basis of within-individual variance and how it affects selection and evolution of the trait

is unclear (but see Mulder *et al.* 2015). The recent development of a framework for its study

22 (Westneat *et al.* 2015; Hill & Mulder 2010) and recent development of statistical methods

Cleasby *et al.* (2015); Mulder *et al.* (2015) should allow for a better understanding of the

24 importance of the variation in within-individual variance.

Currently, one of the biggest problem for the study of within-individual variance differences

is lexical. For trait measured repeatedly in the same environmental conditions, multiple terms

such as intra-individual variability, individual stability, relative specialisation, consistency,

predictability or uniformity are used to refer to variation in within-individual variance (Stamps

et al. 2012; Cleasby *et al.* 2015; Sae-Lim *et al.* 2015). Following, Cleasby *et al.* (2015), we are

using predictability to refer to within-individual variance in a trait in measured repeatedly in the

same environment.

The importance and potential impact of predictability of animal behaviour is now widely

accepted(Réale & Dingemanse 2010; Stamps *et al.* 2012). However, only a handful of estimates

of predictability have been obtained, and often using different non-comparable approaches

(Cleasby *et al.* 2015). The recent development of double hierarchical generalized linear model,

DHGLM, (Lee & Nelder 2006), now allows concurrent estimation of between-individual

differences in the mean of a trait and within-individual variance of that trait at the same time,

while correcting for environmental effects (Cleasby *et al.* 2015). This type of model is an

extension of a mixed-effects model fitting fixed and random effects on both the mean and the

residual variance of a trait (Lee & Nelder 2006; Cleasby *et al.* 2015). In addition, this approach

also allow to obtain comparable parameter of predictability between traits, environments and

species (Hill & Mulder 2010; Cleasby *et al.* 2015).

DHGLM could not only be used to estimate between individual variance in predictability

but using a quantitative genetic approach, the variance in predictability could be decomposed in

its additive genetic and environmental effects (Rönnegård *et al.* 2010; Sae-Lim *et al.* 2015). To

date, only a few estimates of additive genetic variance of predictability have been published and

only captive animal breeding environment (Mulder *et al.* 2015; Hill & Mulder 2010; Sae-Lim

et al. 2015). Despite its potential importance, existence of genetic basis of predictability in any

traits in the wild is unknown. Multiple repeated data for a large number of pedigreed

individuals is needed to be able to use DHGLM in the wild. In addition,the environment should

be measured carefully to ensured that the variation in predictability is not due to uncorrected

environmental variation.

Variation in predictability of a behaviours is emerging as an important aspect of animal personality (Stamps *et al.* 2012; Cleasby *et al.* 2015; Westneat *et al.* 2015). Animal behaviour, such as docility, could be easy traits to measured repeatedly in standardized conditions in the wild. Docility, the reaction to human handling, is a commonly used metric in personality studies, and has been found to be repeatable (ref), heritable (ref), and influence reproduction (ref) in multiple species in the wild. Using long-term trapping data on yellow-bellied, *marmota flaviventris*, we estimated between-individual variation in both mean docility and predictability in docility. Using a quantitative genetic approach, we then implemented a "double hierarchical animal model" to decompose the mean trait and the within-individual variances into their environmental and genetic components.

MATERIAL AND METHODS

Study system

We used behavioural data collected as part of a long-term demographic study on yellow-bellied marmots at the Rocky Mountain Biological Laboratory in Gothic, Colorado, USA (38° 77'N, 106° 59'W). Marmots are large, facultatively social, subalpine rodents that live in colonies consisting of one or more matrilineal groups (Frase & Hoffmann 1980; Armitage 2014). These colonies usually consist of one adult male, multiple adult females, and their offsprings. We regularly trap individuals using Tomahawk live traps (COMPANY?) set at burrow entrances. Once trapped, individuals were weighed, sexed, their ano-genital distance and left hind foot measured, ear tagged, and given an unique dye mark to facilitate identification from afar (Blumstein *et al.* 2009).

Docility was assessed as an individual's reaction to being trapped and handled (Réale *et al.* 2007; Petelle *et al.* 2013). Upon arriving at a trap, individuals were placed inside a

cloth-handling bag, and we dichotomously scored (0, 1) whether individuals bit the trap,

emitted an alarm called, struggled in the trap or bag, tooth chattered, and whether they hesitated

moving from the trap into the handling bag. We summed these scores and subtracted them from

a maximum of five. Thus, a docile individual would have a score of five while an individual

with a score of 0 would be non-docile or pugnacious (Réale *et al.* 2007). We quantified docility

over 11,389 trapping events for 1,576 individuals of known age and sex from 2002-2014. Mean

and range of docility observations varied widely across individuals (Fig. S1).

Parentage was assigned from DNA samples collected from individuals during their first

trapping event. We extracted DNA using a QiaGen QIAamp DNA minikit and genotyped

individuals using 12 microsatellites. Alleles were visualized and assigned using GeneMapper

4.1 software (Applied Biosystems). CERVUS (Kalinowski *et al.* 2007) was then used to assign

maternity and paternity using a maximum likelihood method at 95% confidence for the trio. All

adult males and females in a colony were used as potential parents. Genetic assignments of

maternity confirmed behavioural observations based on juveniles emergence from maternal

burrow. For full details on the pedigree reconstruction method see Olson *et al.* (2012) and

Blumstein *et al.* (2010). The pedigree used in these analyses included 1588 individuals with

90% and 83% of the maternal and paternal links known respectively (see Table S1 for detailed

pedigree structure information).

Statistical analysis

The aim of our analysis was to concurrently estimate the between-individual differences in

mean docility and its residual within-individual variance. Moreover, we wanted to decompose

the variability of the mean trait and of its variance into environmental and genetic components

using a quantitative genetic approach. We developed four models differing in their random and

residual structure that progressively built towards such goal, while allowing us to monitor any

change in the estimates as increasing complexity was introduced (see Table 1). Following

previous results from this population (Petelle *et al.* 2013; 2015), we included the following

fixed effects in the mean part of all models: trial number, to account for potential habituation to

human handling; day of the year, as a proxy for any seasonal changes in docility; time of day,

coded as 0 for AM sampling and 1 for PM sampling; and age, which was a categorical factor

with three levels (juveniles, yearlings and adults).

Model 1 was a traditional mixed-effects model, where the mean docility was modelled as a

combination of fixed and random effects and variance was assumed to be homogeneous across

individuals. Model 1 can be therefore written as:

$$\boldsymbol{Y} = \boldsymbol{X_m}\boldsymbol{b_m} + \boldsymbol{M}\boldsymbol{yr_m} + \boldsymbol{Z}\boldsymbol{pe_m} + \boldsymbol{e} \tag{1}$$

where $\boldsymbol{yr_m} \sim N(0, \boldsymbol{I}\sigma^2_{yr_m})$, $\boldsymbol{pe_m} \sim N(0, \boldsymbol{I}\sigma^2_{pe_m})$ and $\boldsymbol{e} \sim N(0, \boldsymbol{I}\sigma^2_e))$. $\boldsymbol{Y}$ is the vector of

docility records. $\boldsymbol{b_m}$, $\boldsymbol{yr_m}$ and $\boldsymbol{pe_m}$ are the vectors of fixed, random year and permanent

environmental (identity) effects associated with the corresponding incidence matrix $\boldsymbol{X_m}$, $\boldsymbol{M}$

and $\boldsymbol{Z}$. $\boldsymbol{e}$ is the vector of residuals with variance σ^2_e. $\sigma^2_{yr_m}$ and $\sigma^2_{pe_m}$ are the between-year and

between-individual random effect variances, respectively. $\boldsymbol{I}$ is the identity matrix.

Similarly to model 1, model 2 only considered changes in mean docility. However, this

model also included an additive genetic component, fitted as a random effect on the mean

(Waldmann 2009). Model 2 is therefore equivalent to a classic animal model (Kruuk 2004), and

can be written as:

$$\boldsymbol{Y} = \boldsymbol{X_m}\boldsymbol{b_m} + \boldsymbol{M}\boldsymbol{yr_m} + \boldsymbol{Z}\boldsymbol{pe_m} + \boldsymbol{Z}\boldsymbol{a_m} + \boldsymbol{e} \tag{2}$$

where, building on equation 1, $\boldsymbol{a_m} \sim N(0, \boldsymbol{A}\sigma^2_{a_m})$. $\boldsymbol{a_m}$ is the vector of additive genetic effects.

Since each individual has an additive genetic as well as a permanent environmental effect, both

effects have the same design matrix $\boldsymbol{Z}$. $\sigma^2_{a_m}$ is the additive genetic variance of the mean trait

and $\boldsymbol{A}$ is the additive genetic relationship matrix.

Model 3 was a double hierarchical generalised linear model (DHGLM) (Lee & Nelder

2006; Cleasby *et al.* 2015). This included a model for the mean docility (as in model 1), as well

as a dispersion part for the residual variance. Following SanCristobal-Gaudy *et al.* (1998), the

residual variance was modelled on the log-normal scale as a function of the fixed effect of age,

with year and individual identity as random effects. We also estimated the correlation between

the individual random effect on the mean and on the within-individual variance, using a

multivariate Normal distribution. Model 3 can be written as:

$$Y = X_m b_m + M y r_m + Z p e_m + e$$
$$\log(\sigma_e^2) = X_v b_v + M y r_v + Z p e_v \tag{3}$$

where $e \sim N\left(0, Diag[\sigma_e^2]\right)$, $yr_v \sim N\left(0, I\sigma_{yr_{v,exp}}^2\right)$, $\begin{bmatrix} pe_m \\ pe_v \end{bmatrix} \sim N \left(\begin{matrix} 0 \\ 0 \end{matrix}, \Sigma_{pe} \otimes I \right)$ and

$\Sigma_{pe} = \begin{bmatrix} \sigma_{pe_m}^2 & \sigma_{pe_m}\sigma_{pe_{v,exp}}\rho_{pe} \\ \sigma_{pe_m}\sigma_{pe_{v,exp}}\rho_{pe} & \sigma_{pe_{v,exp}}^2 \end{bmatrix}$. Building on equation 1, σ_e^2 is now a vector and

$Diag()$ is used to create a diagonal matrix. b_v, yr_v and pe_v are the vectors of fixed, random

year and random permanent environmental (identity) effects associated with the corresponding

incidence matrix X_v, M and Z. $\sigma_{yr_{v,exp}}^2$ and $\sigma_{pe_{v,exp}}^2$ are the year and permanent environmental

variance of the within-individual variance on the exponential scale. ρ_{pe} is the correlation at the

individual level between the mean trait and the within-individual variance of the trait.

Finally, model 4 was a double hierarchical generalised linear "animal" model (DHGLAM),

with a mean and a dispersion part as in model 3, but including an additive genetic component

(as in model 2) fitted as a correlated random effect on both the mean and the within-individual

variance (Felleki *et al.* 2012). Starting from Equation 3, model 4 can therefore be written as:

$$Y = X_m b_m + M y r_m + Z p e_m + Z a_m + e$$
$$\log(\sigma_e^2) = X_v b_v + M y r_v + Z p e_v + Z a_v \tag{4}$$

where $\begin{bmatrix} \boldsymbol{a_m} \\ \boldsymbol{a_v} \end{bmatrix} \sim N \left(\begin{matrix} 0 \\ 0 \end{matrix}, \Sigma_a \otimes \boldsymbol{A} \right)$ and $\Sigma_a = \begin{bmatrix} \sigma_{a_m}^2 & \sigma_{a_m}\sigma_{a_{v,exp}}\rho_a \\ \sigma_{a_m}\sigma_{a_{v,exp}}\rho_a & \sigma_{a_{v,exp}}^2 \end{bmatrix}$. $\boldsymbol{a_v}$ is the vectors

of additive genetic effects associated with the corresponding incidence matrix $\boldsymbol{Z}$. $\sigma_{a_{v,exp}}^2$ is the additive genetic variance of the within-individual variance on the exponential scale and ρ_a is the additive genetic correlation between the mean and within-individual variance.

The estimated variance components ($\sigma_{yr_{v,exp}}^2$, $\sigma_{pe_{v,exp}}^2$ and $\sigma_{a_{v,exp}}^2$) for within-individual variance of docility were on the exponential scale (exp) and were converted to an additive scale ($\sigma_{yr_v}^2$, $\sigma_{pe_v}^2$ and $\sigma_{a_v}^2$) using the equations derived by Mulder *et al.* (2007) (see also Appendix 3). For each model, we estimated the phenotypic variance conditioned on the fixed effects (σ_P^2) as the sum of the variance components and the residual variance (σ_e^2). For model 3 and 4, σ_e^2 was estimated as $\exp\left(b_{v_0} + \frac{b_{v_1}}{3} + \frac{b_{v_2}}{3}\right) \exp\left(\frac{\sigma_{yr_{v,exp}}^2}{2}\right) \exp\left(\frac{\sigma_{pe_{v,exp}}^2}{2}\right) \exp\left(\frac{\sigma_{a_{v,exp}}^2}{2}\right)$ (Appendix 3; Felleki *et al.* 2012; Sae-Lim *et al.* 2015). For all models, repeatability (or permanent environment effect, pe^2) for mean docility was estimated as $\frac{\sigma_{pe_m}^2}{\sigma_P^2}$ and for within-individual variance in docility (pe_v^2) as $\frac{\sigma_{pe_v}^2}{2\sigma_P^4 + 3(\sigma_{yr_v}^2 + \sigma_{pe_v}^2 + \sigma_{a_v}^2)}$. Similarly heritability of docility (h^2) and of within-individual variance in docility (h_v^2) were estimated as $\frac{\sigma_{a_m}^2}{\sigma_P^2}$ and $\frac{\sigma_{a_v}^2}{2\sigma_P^4 + 3(\sigma_{yr_v}^2 + \sigma_{pe_v}^2 + \sigma_{a_v}^2)}$, respectively (Appendix 3; Mulder *et al.* 2007). We also reported the permanent environment and genetic coefficient of variation of the within-individual variance on the additive scale estimated as $CV_{pe_v} = \frac{\sigma_{pe_v}}{\sigma_e^2}$ and $CV_{a_v} = \frac{\sigma_{a_v}}{\sigma_e^2}$ respectively (Hill & Mulder 2010). It should be noted that the equation in Cleasby *et al.* (2015) for the coefficient of variation estimated on the exponential scale is valid only with 1 random effect for the within-individual variance (i.e. dispersion part of the model).FiXme: not sure if we need that

The four models were fitted in a Bayesian framework using OpenBUGS 3.2.1 (Thomas *et al.* 2006), run from R (R Development Core Team 2014) via the package R2OpenBUGS Sturtz *et al.* (2005). Quantitative genetic effects were implemented in BUGS following Waldmann (2009) and Gorjanc (2010). We used Normal priors with mean 0 and precision 0.001 for the fixed effects in both the mean and dispersion part. σ_e had a uniform prior

$U(0, 20)$, and σ_{yr_m} and σ_{yr_v} had uniform priors $U(0, 10)$. In model 1 and 2, σ_{pe_m} had a uniform

prior $U(0, 10)$, while in model 3 and 4, Σ_{pe} had an inverse Wishart prior with 3 degrees of

freedom and scale matrix $\begin{bmatrix} 1 & 0 \\ 0 & 1 \end{bmatrix}$. In model 2, σ_{a_m} had a uniform prior $U(0, 15)$, while for Σ_a

in model 4, we used an inverse Wishart prior with 3 degrees of freedom and scale matrix

$\begin{bmatrix} 1 & 0 \\ 0 & 1 \end{bmatrix}$. The OpenBUGS code for model 4 is provided in the Supplementary material

(ESM 2). Markov Chain Monte Carlo (MCMC) algorithms were iterated until convergence to

the joint posterior distribution. Three chains starting at different initial values were run in

parallel. Convergence was first assessed by visually inspecting the trace plots, which were also

used to identify an appropriate number of burn-in iterations. Each chain ran for 270,000

iterations including 70,000 burn-in iterations. We then checked that the Monte Carlo error was

less than 1-5% of the posterior standard deviation, and that the Brooks-Gelman-Rubin (BGR)

diagnostic converged to 1 ± 0.2 Gilks *et al.* (1995). These convergence checks were carried out

using the package coda (Plummer *et al.* 2006) in R. The mode and 95% Highest Posterior

Density Intervals (HPDI) were used to summarise the posterior distributions of the model

parameters. Results are reported using the combined 600,000 iterations from the 3 unthinned

chains following (Link & Eaton 2012; Kruschke 2014).

RESULTS

We found that parameter estimates for both fixed and random effects across all models were

highly consistent (Fig. 1), Table 2) validating the approach used. Trial number and age had a

significant effect on the mean part of all models (estimated as 95% HDPI not overlapping zero).

Age was also significant in the dispersion part of both model 3 and 4 (Fig. 1). However, time of

the day had no significant effect when also modelling the dispersion of docility (model 3 and 4,

Fig. 1).

As previously reported (Petelle *et al.* 2015), we found significant repeatability (pe^2) and heritability (h^2) of docility (Table 2) with similar estimates when comparing hierarchical models (models 1, 2) with double hierarchical models (models 3, 4). More importantly, we found significant permanent environment and additive genetic variance in the within-individual variance of docility (Fig. 1, Table 2) with estimated repeatability (pe_v^2) and heritability (h_v^2) equal to 0.09 (95%HPDI: 0.07/0.11) and 0.07 (0.05/0.10) respectively. In addition, both permanent environment and additive genetic correlation between the mean and the within individual variance were negative and significantly different from zero (Fig. 1, Table 2).

Permanent environment variance (σ_{pe}^2) for the mean is consistent across model 1 and 3, and across model 2 and 4 (Fig. 1, Table 2). The difference in (σ_{pe}^2) between models 1, 3 and models 2, 4 results from the addition of the additive genetic effect in models 2 and 4. In models 2 and 4, the sum of the additive genetic (σ_a^2) and permanent environmental (σ_{pe}^2) variances are consistent with the estimates of (σ_{pe}^2) in model 1 and 3 indicating that the models are behaving adequately (Table 2). As with the mean part of the model, the sum of the additive genetic ($\sigma_{a_v}^2$) and permanent environmental ($\sigma_{pe_v}^2$) variances in the dispersion part of model 4 are consistent with the estimates of ($\sigma_{pe_v}^2$) in model 3 (Table 2).

The random effect of year was negligible in both the mean and the dispersion part of the models (Fig. 1, Table 2). We then refitted the models without year as a random effect in either the mean or the dispersion part of the model Table S2 and found both qualitatively and quantitatively similar results (Fig. S2 and Table S3).

DISCUSSION

FiXme: need to be written

These analyses are the first to estimate the genetic basis of both mean trait and within-individual variance in a trait in a wild population. Our results indicate that equal within-individual variance should not be assumed. We show heritable within-individual

variance of a behaviour. We also illustrate that heritability and other variance ratio could be estimated using such models and argued that they should be used over other estimates (Stamps or Cleasby or Reale) In addition, we demonstrate the evolutionary importance of considering variation in within-individual variance in traits, because the positive genetic covariance between the mean trait and within-individual variance can influence the evolutionary trajectory of docility. Work by Mulder 2015 suggest non linear response to linear selection on mean trait if mean-variance in the trait is genetically correlated. heritability of the within-individual variance is estimated based on the assumption that the correlation is 0 so its use in selection analysis should be done carefully. full equation is available in Mulder *et al.* (2007).

For the moment the full implication of genetic within-individual variance on trait selection and evolution is not fully understood. Promising area of new research.

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TABLES

Table 1 Fixed and random effects fitted in each model of docility in yellow-bellied marmots at RMBL. ID represents a permanent environmental effects whereas AG represents additive genetic effects.

|	Mean part effects		Dispersion part effects	
Model	Fixed	Random	Fixed	Random
1	Trial + Date + Time + Age	Year + ID		
2	Trial + Date + Time + Age	Year +ID + AG		
3	Trial + Date + Time + Age	Year + ID	Age	Year + ID
4	Trial + Date + Time + Age	Year + ID + AG	Age	Year + ID + AG

Table 2 Estimates of variance components and variance ratios of docility for the four different models differing in their random and residual structure (see table 1). Analysis used 11,389 observations from 1,576 individuals between 2002-2014.

	Models			
	1	2	3	4
σ^2_P	0.872 (0.903/0.999)	0.959 (0.918/1.004)	0.995 (0.892/1.126)	1.251 (1.075/1.494)
Mean part				
σ^2_{yr}	0.003 (0.005/0.059)	0.012 (0.004/0.038)	0.012 (0.005/0.038)	0.01 (0.004/0.031)
σ^2_{pe}	0.215 (0.185/0.243)	0.099 (0.073/0.129)	0.18 (0.16/0.205)	0.105 (0.083/0.128)
σ^2_a	-	0.132 (0.09/0.18)	-	0.097 (0.069/0.132)
$year^2$	0.016 (0.006/0.061)	0.013 (0.005/0.039)	0.012 (0.005/0.037)	0.008 (0.003/0.024)
pe^2	0.227 (0.196/0.256)	0.102 (0.075/0.135)	0.183 (0.156/0.208)	0.081 (0.059/0.107)
h^2	-	0.14 (0.096/0.183)	-	0.078 (0.055/0.103)
Dispersion part				
$\sigma^2_{yr_{v,exp}}$	-	-	0.03 (0.011/0.092)	0.026 (0.01/0.086)
$\sigma^2_{pe_{v,exp}}$	-	-	0.657 (0.577/0.749)	0.391 (0.304/0.484)
$\sigma^2_{a_{v,exp}}$	-	-	-	0.289 (0.189/0.418)
$year^2_v$	-	-	0.007 (0.003/0.021)	0.007 (0.002/0.02)
pe^2_v	-	-	0.154 (0.139/0.171)	0.093 (0.073/0.115)
h^2_v	-	-	-	0.069 (0.046/0.098)
CV_{year_v}	-	-	0.030 (0.011/0.114)	0.040 (0.013/0.141)
CV_{pe_v}	-	-	0.730 (0.584/0.984)	0.587 (0.425/0.818)
CV_{a_v}	-	-	-	0.421 (0.243/0.737)
Covariance				
cov_{pe}	-	-	-0.324 (-0.364/-0.293)	-0.183 (-0.225/-0.144)
cov_a	-	-	-	-0.149 (-0.208/-0.096)
cor_{pe}	-	-	-0.944 (-0.958/-0.929)	-0.907 (-0.931/-0.871)
cor_a	-	-	-	-0.876 (-0.919/-0.811)

σ^2_P = estimated phenotypic variance. σ^2_a and $\sigma^2_{a_{v,exp}}$ = additive genetic variance for mean docility and within-individual variance in docility on the exponential scale, respectively. σ^2_{pe}= permanent environmental variance, σ^2_{yr} = year variance. h^2 and h^2_v = heritability for mean docility and within-individual variance in docility, respectively. pe^2 = permanent environmental (2 and 4) or repeatability (1 and 3) estimates. $year^2$ = year effect. CV_{year_v}, CV_{pe_v} and CV_{a_v} are the coefficient of variance for the within-individual variance effects.

FIGURES

Figure 1 Posterior mode and 95% credible intervals for four different models of docility of Yellow-bellied marmots at RMBL. Analysis used 11,389 observations from 1,576 individuals over between 2002-2014. Grey shaded area illustrates an invalid region of the parameter space. Residual variance (σ_e^2) for models 3 and 4 were estimated based on Appendix 3. Juvenile was considered as references in both mean and variance part of the model. 3.7 was subtracted from the estimates of the intercept to facilitate plotting
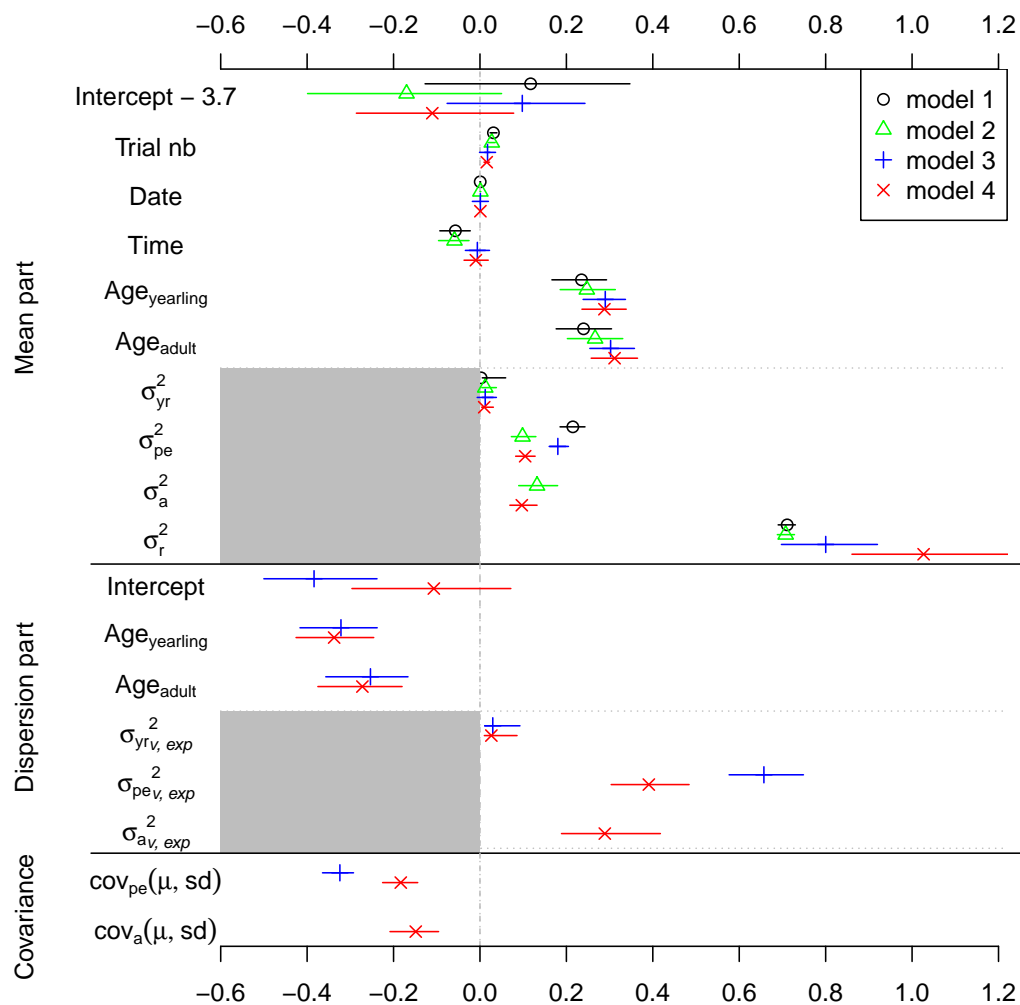
ELECTRONIC SUPPLEMENTARY MATERIALS

2   Appendix S1. Supplementary tables and figures

Appendix S2. Annotated code to fit model 4 in OpenBugs (File: model4_bugs.r)

4   Appendix S3. Calculation of variance components and variance ratios for (exponential) double

hierarchical models.

6   **1   Supplementary tables and figures**

Table S1 Estimates of variance components and variance ratios of docility for the four different
models differing in their random and residual structure (see table 1). Analysis used 11,389
observations from 1,576 individuals between 2002-2014.

Variable	Value
Records	1588
Maternities	1436
Paternities	1320
Full sibs	5335
Maternal sibs	10960
Maternal half sibs	5625
Paternal sibs	31312
Paternal half sibs	25977
Maternal grandmothers	1156
Maternal grandfathers	926
Paternal grandmothers	660
Paternal grandfathers	614
Maximum pedigree depth	10
Founders	145
Mean maternal sibship size	8.975
Mean maternal sibship size	17.600
Non-zero F	511
F>0.125	278
Mean pairwise relatedness	0.045
Pairwise relatedness >=0.125	0.146
Pairwise relatedness >=0.25	0.081
Pairwise relatedness >=0.5	0.017

Table S2 Fixed and random effects fitted in each model of docility in yellow-bellied marmots at RMBL. ID represents a permanent environmental effects whereas AG represents additive genetic effects.

| Model | Mean part effects | | Dispersion part effects | |
	Fixed	Random	Fixed	Random
1	Trial + Date + Time + Age	ID		
2	Trial + Date + Time + Age	ID + AG		
3	Trial + Date + Time + Age	ID	Age	ID
4	Trial + Date + Time + Age	ID + AG	Age	ID + AG

Table S3 Estimates of variance components and variance ratios of docility for the four different models differing in their random and residual structure (see table S2). Analysis used 11,389 observations from 1,576 individuals over between 2002-2014.

| | Models | | | |
	1	2	3	4
σ^2_P	0.951 (0.918/0.985)	0.966 (0.925/1.006)	0.984 (0.927/1.057)	1.248 (1.108/1.455)
Mean part				
σ^2_{pe}	0.236 (0.208/0.269)	0.101 (0.072/0.13)	0.198 (0.173/0.22)	0.105 (0.085/0.131)
σ^2_a	-	0.150 (0.105/0.199)	-	0.108 (0.075/0.140)
pe^2	0.251 (0.225/0.276)	0.106 (0.075/0.136)	0.198 (0.179/0.219)	0.083 (0.062/0.108)
h^2	-	0.156 (0.113/0.202)	-	0.084 (0.061/0.108)
Dispersion part				
$\sigma^2_{pe_{v,exp}}$	-	-	0.696 (0.607/0.786)	0.412 (0.321/0.504)
$\sigma^2_{a_{v,exp}}$	-	-	-	0.296 (0.196/0.421)
pe^2_v	-	-	0.162 (0.148/0.179)	0.099 (0.078/0.121)
h^2_v	-	-	-	0.071 (0.049/0.1)
Covariance				
cov_{pe}	-	-	-0.348 (-0.388/-0.314)	-0.188 (-0.232/-0.15)
cov_a	-	-	-	-0.155 (-0.218/-0.104)
cor_{pe}	-	-	-0.949 (-0.96/-0.933)	-0.908 (-0.933/-0.875)
cor_a	-	-	-	-0.885 (-0.922/-0.82)

σ^2_P = estimated phenotypic variance. σ^2_a and $\sigma^2_{a_{v,exp}}$ = additive genetic variance for mean docility and within individual variance in docility on the exponential scale, respectively. σ^2_{pe}= permanent environmental variance. h^2 and h^2_v = heritability for mean docility and variance in docility, respectively. pe^2 = permanent environment (2 and 4) or repeatability (1 and 3) estimates.

.

Figure S1 Mean (point) and range (dotted line) of docility for 1576 yellow-bellied marmots at RMBL between 2002-2014.
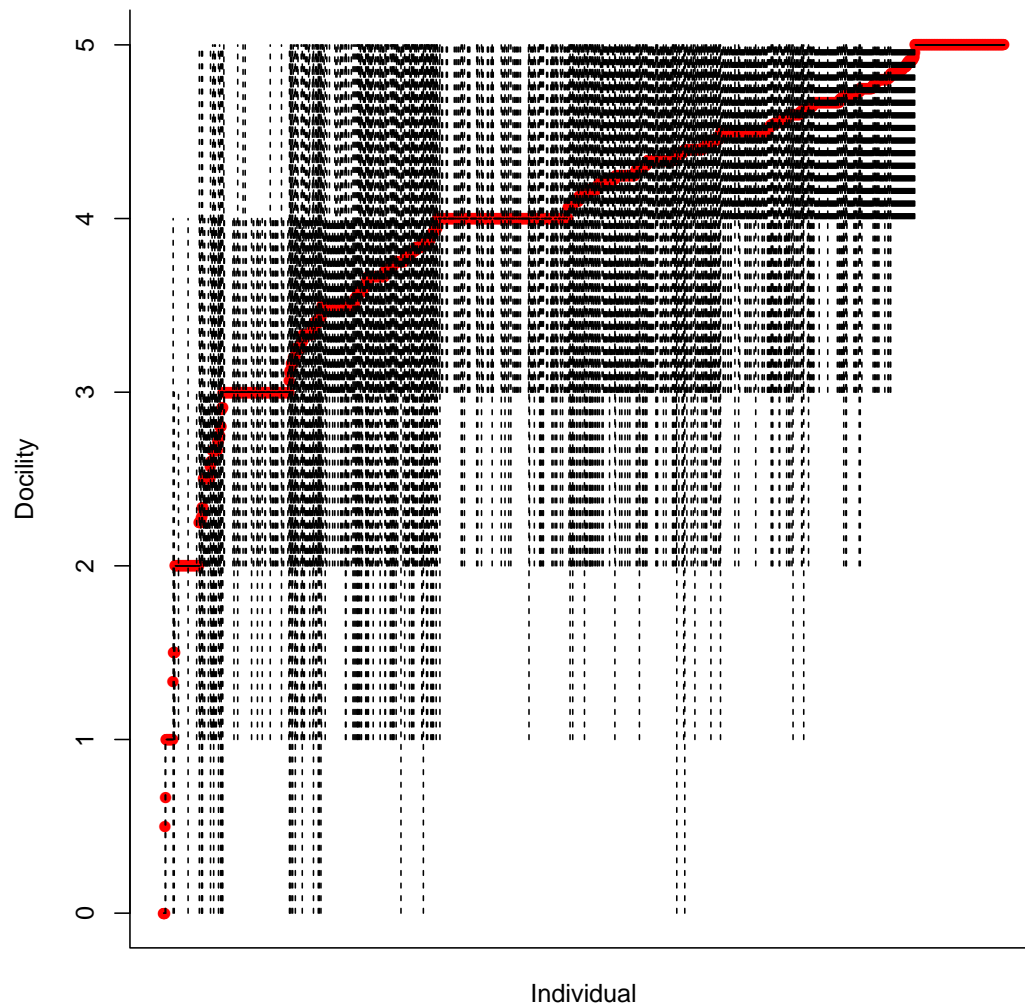
Figure S2 Posterior mode and 95% credible intervals for four different models of docility of Yellow-bellied marmots at RMBL. Analysis used 11,389 observations from 1,576 individuals over 13 years. Grey shaded area illustrates an invalid region of the parameter space. Residual variance (σ_e^2) for models 3 and 4 were estimated based on Appendix 3. Juvenile was considered as references in both mean and variance part of the model. 3.7 was subtracted from the estimates of the intercept to facilitate plotting.
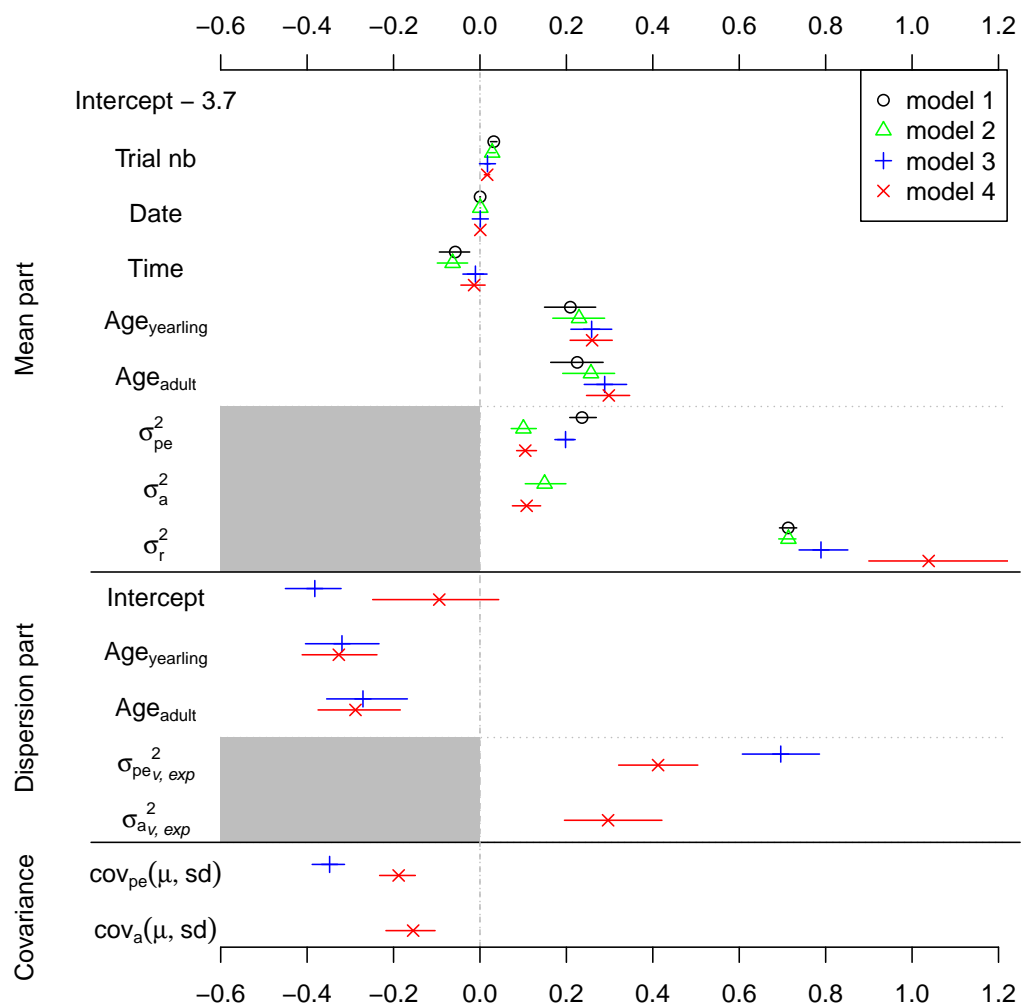
2 Annotated code to fit model 4 in OpenBugs

2 The code is also available in the file model4_bugs.r

```
model{
#priors
## fixed effects: b, bv
for(h in 1:6){                          #for the mean part
        b[h] ~ dnorm(0, 0.001)
        }
for(s in 1:3){                          #for the dispersion part
        bv[s] ~ dnorm(0, 0.001)
        }
##random effects
###year
####for the mean part
sdyearmu ~ dunif(0,10)                  #prior on standard deviation
tauyearmu <- 1/sdyearmu/sdyearmu        #conversion to a precision
s2yearmu <- sdyearmu * sdyearmu         #variance estimate
####for the dispersion part
sdyearV ~ dunif(0,10)                   #prior on standard deviation
tauyearV <- 1/sdyearV/sdyearV           #conversion to a precision
s2yearV <- sdyearV * sdyearV            #variance estimate
for (y in 1:n.years){                   #values for each year
        yearmu[y] ~ dnorm(0, tauyearmu)
        yearV[y] ~ dnorm(0, tauyearV)
        }
###permanent environmental effect(indivual identity)
taupe[1:2,1:2] ~ dwish(matpe[,],3) #wishart prior on the precision matrix
s2pe[1:2,1:2] <- inverse(taupe[,]) #conversion to a variance matrix
for (m in 1:n.id){                      #values for each individual
        pe[m,1:2] ~ dmnorm(zero[], taupe[,])
```

```
            }
2  ###Additive genetic effects
   tauag[1:2,1:2] ~ dwish(matag[,],3) #wishart prior on the precision matrix
4  s2ag[1:2,1:2] <- inverse(tauag[,]) #conversion to a variance matrix
   ####values for each founder (no known parents)
6  for (k in 1:n.fnd){
           ag[k,1:2] ~ dmnorm(matag[], tauag[,])
8          }
   ####individuals with only father unknown
10 for (u in 1:nfunk){
           #unknown father breeding value
12         agfunk[u,1:2] ~ dmnorm(matag[], tauag[,])
           #mid-parent value for both mean and dispersion
14         parag[funk[u],1] <- (ag[mid[funk[u]],1] + agfunk[u,1])/2
           parag[funk[u],2] <- (ag[mid[funk[u]],2] + agfunk[u,2])/2
16         #breeding values
           agi[funk[u],1:2] ~ dmnorm(parag[funk[u],1:2], tauag[,])
18         ag[funk[u],1] <- agi[funk[u],1] * wsq[funk[u]]
           ag[funk[u],2] <- agi[funk[u],2] * wsq[funk[u]]
20         }
   ####individuals with only mother unknown
22 for (uu in 1:n.munk){
           #unknown mother breeding value
24         agmunk[uu,1:2] ~ dmnorm(matag[], tau.ag[,])
           #mid-parent value for both mean and dispersion
26         parag[munk[uu],1] <- (ag[fid[munk[uu]],1] + agmunk[uu,1])/2
           parag[munk[uu],2] <- (ag[fid[munk[uu]],2] + agmunk[uu,2])/2
28         #breeding values
           agi[munk[uu],1:2] ~ dmnorm(parag[munk[uu],1:2], tauag[,])
30         ag[munk[uu],1] <- agi[munk[uu],1] * wsq[munk[uu]]
           ag[munk[uu],2] <- agi[munk[uu],2] * wsq[munk[uu]]
```

```
        }
####individuals with both parents known
for (d in 1:n.des){
        #mid-parent value for both mean and dispersion
        parag[des[d],1] <- (ag[fid[des[d]],1] + ag[mid[des[d]],1])/2
        parag[des[d],2] <- (ag[fid[des[d]],2] + ag[mid[des[d]],2])/2
        #breeding values
        agi[des[d],1:2] ~ dmnorm(parag[des[d],1:2],tau.ag[,])
        ag[des[d],1] <- agi[des[d],1] * wsq[des[d]]
        ag[des[d],2] <- agi[des[d],2] * wsq[des[d]]
        }
#Likelihood
for(i in 1:n){
        #each observation has its own mean and precision
        docility[i] ~ dnorm(muy[i], tauerr[i])
        #express the model in terms of the variance
        tauerr[i] <- 1/s2y[i]
## Model for the mean (Mean part)
        muy[i] <- b[1] + b[2]*trial[i] + b[3]*day[i] + b[4]*time[i] + b[5]*
   age1[i] + b[6]*age2[i] + yearmu[year[i]] + pe[id[i],1] + ag[id[i],1]
## Model for the variance (Dispersion part)
        log(s2y[i]) <- bv[1] + bv[2]*age1[i] + bv[3]*age2[i] + yearV[year[i
   ]] + pe[id[i],2] + ag[id[i],2]
        }
}
```

3   Calculation of variance ratios for double hierarchical models.

The aim here is to show the extension of the method presented in (Mulder *et al.* 2007) to multiple random effects and how other parameters can be calculated. Felleki *et al.* (2012) and Sae-Lim *et al.* (2015) showed derivations to estimate the heritability and permanent environment effect for within-individual variance. Using their approach, we reported their equations to estimate similar parameter when 3 random effects are included in the dispersion part of the model. First, it should be noted that the double hierarchical animal model (equation 4) could also be written in an additive way allowing an easier understanding of the estimations of the variance components and their ratios (SanCristobal-Gaudy *et al.* 1998).

$$
\begin{aligned}
\boldsymbol{Y} = &\boldsymbol{X_m b_m} + \boldsymbol{M y r_m} + \boldsymbol{Z p e_m} + \boldsymbol{Z a_m} \\
&+ \chi \exp[1/2(\boldsymbol{X_v b_v} + \boldsymbol{M y r_v} + \boldsymbol{Z p e_v} + \boldsymbol{Z a_v})]
\end{aligned}
\tag{5}
$$

where $\chi \sim N(0,1)$ is a normal deviate.

The residual variance σ_e^2 is calculated as:

$$
\sigma_e^2 = \sigma_{e,exp}^2 \exp\left(\frac{\sigma_{yr_v,exp}^2}{2}\right) \exp\left(\frac{\sigma_{pe_v,exp}^2}{2}\right) \exp\left(\frac{\sigma_{a_v,exp}^2}{2}\right)
\tag{6}
$$

In our analysis, the dispersion part of the model included three age categories as fixed effect. Thus assuming that the three age categories are equally represented in the sample, we can estimate $\sigma_{e,exp}^2$ as $\left(b_{v_0} + \frac{b_{v_1}}{3} + \frac{b_{v_2}}{3}\right)$. The sum of the genetic, permanent environmental and year variance for the additive model can be calculated as:

$$
\sigma_{a_v}^2 + \sigma_{pe_v}^2 + \sigma_{yr_v}^2 = \sigma_{e,exp}^4 \exp(2\sigma_{a_v,exp}^2) \exp(2\sigma_{pe_v,exp}^2) \exp(2\sigma_{yr_v,exp}^2) - \sigma_e^4
\tag{7}
$$

The product of equation (2) is a combination of $\sigma_{a_v}^2$, $\sigma_{pe_v}^2$ and $\sigma_{yr_v}^2$. Under the assumption that the ratio of $\frac{\sigma_{a_v}^2}{\sigma_{a_v}^2 + \sigma_{pe_v}^2 + \sigma_{yr_v}^2}$ is equal on both the additive and exponential scales, $\sigma_{a_v}^2$ is

calculated as:

$$\sigma^2_{a_v} = (\sigma^2_{yr_v} + \sigma^2_{pe_v} + \sigma^2_{a_v})\frac{\sigma^2_{a_{v,exp}}}{\sigma^2_{yr_{v,exp}} + \sigma^2_{pe_{v,exp}} + \sigma^2_{a_{v,exp}}} \tag{8}$$

2   Similarly, $\sigma^2_{pe_v}$ and $\sigma^2_{yr_v}$ are estimated as:

$$\sigma^2_{pe_v} = (\sigma^2_{yr_v} + \sigma^2_{pe_v} + \sigma^2_{a_v})\frac{\sigma^2_{pe_{v,exp}}}{\sigma^2_{yr_{v,exp}} + \sigma^2_{pe_{v,exp}} + \sigma^2_{a_{v,exp}}} \tag{9}$$

$$\sigma^2_{yr_v} = (\sigma^2_{yr_v} + \sigma^2_{pe_v} + \sigma^2_{yr_v})\frac{\sigma^2_{yr_{v,exp}}}{\sigma^2_{a_{v,exp}} + \sigma^2_{pe_{v,exp}} + \sigma^2_{yr_{v,exp}}} \tag{10}$$

Variance ratios including heritability (h^2) and repeatability (r^2) are important parameters in

4   ecology and evolution (Lynch & Walsh 1998; Roff 2002). To ease comparison with other traits

and standardize results of heterogeneity of within-individual variance, Mulder *et al.* (2007)

6   defined a measure of heritability (h^2_v) for the within-individual variance in a trait. They

proposed that (h^2_v) equals the genetic variance in within-individual variance as a proportion of

8   the variance of the square of the trait, P^2. Thus, the heritability for within-individual variance

(h^2_v) can be calculated as:

$$h^2_v = \frac{\sigma^2_{a_v}}{2\sigma^4_P + 3(\sigma^2_{yr_v} + \sigma^2_{pe_v} + \sigma^2_{a_v})} \tag{11}$$

10   Similarly, permanent environment (pe^2) and year ($year^2$) can be calculated as:

$$pe^2_v = \frac{\sigma^2_{pe_v}}{2\sigma^4_P + 3(\sigma^2_{yr_v} + \sigma^2_{pe_v} + \sigma^2_{a_v})} \tag{12}$$

$$year^2_v = \frac{\sigma^2_{yr_v}}{2\sigma^4_P + 3(\sigma^2_{yr_v} + \sigma^2_{pe_v} + \sigma^2_{a_v})} \tag{13}$$

For these equations, it is assumed that genetic (r_a) and permanent environmental (r_{pe})

12   correlations between mean and within individual variance are 0, otherwise the denominator

would be slightly higher with the exponential model (Mulder *et al.* 2007). Even if the effect of

14   this simplifying assumption seems to be weak (Mulder *et al.* 2007; Sae-Lim *et al.* 2015), h^2_v

should be used only as a first approximation in standard prediction evolutionary model when

$r_a = 0$.