

## Supplementary Information

Throughout this document, when the mean and variance of the Normal distribution probability and cumulative density functions are not mentioned, they are assumed equal to 0 and 1, respectively for the mean and variance. Hence, by default,  $f_{\mathcal{N}}(\ell)$  and  $\Phi_{\mathcal{N}}(\ell)$  correspond to a standard Normal distribution.

### A Proof for analytical solutions for binary traits

**Equivalence between a Binomial/Probit GLMM and the threshold model** We consider the probability of the observed data  $z$  to be 1, knowing that the latent trait value is  $\ell$  (hence from the GLMM perspective):

$$P(z = 1) = \Phi_{\mathcal{N}}(\ell) = P(X < \ell) = P(0 < \ell - X), \quad (\text{S1})$$

where  $X$  is a random variable following a standard Normal distribution. Let  $\epsilon$  be a variable such that  $\epsilon = -X$ , then  $\epsilon$  also follows a standard Normal distribution. This allows us to rewrite the above equation as:

$$P(z = 1) = P(0 < \ell + \epsilon), \quad (\text{S2})$$

which is the probability defined from the threshold model perspective. The addition of the  $\epsilon$  term, which has a variance of 1, explains the appearance of the so-called ‘‘link variance’’. Note that the exact same reasoning apply to the logit link function, which inverse function is the cumulative distribution function of a logistic distribution of location 0 and scale 1. Thus, the ‘‘link variance’’ associated with a logit link is  $\pi^3/2$ .

**Observed phenotypic mean** Let  $p$  be the average phenotype (as well as the probability of 1, which is an equivalent definition). Note that because of the equivalence between the GLMM and the threshold model:

$$p = \int \Phi_{\mathcal{N}}(\ell) f_{\mathcal{N}}(\ell, \mu, V_{\text{P}}) d\ell = 1 - \Phi_{\mathcal{N}}(0, \mu, V_{\text{P}} + 1), \quad (\text{S3})$$

which provides a quick analytical way to compute  $p$ . If fixed effects are included in the model,  $p$  is simply this calculation averaged over the elements of  $\mathbf{X}\hat{\mathbf{b}}$ :

$$p = 1 - \frac{1}{N} \sum_i \Phi_{\mathcal{N}}(0, \mu + (\mathbf{X}\hat{\mathbf{b}})_i, V_{\text{P}} + 1). \quad (\text{S4})$$

**Observed phenotypic variance** The observed variance of the phenotype only depends on the mean  $p$  and is  $p(1 - p)$ . This is a property of a binomial distribution with only one trial and is consistent with Eq. ??:

$$\begin{aligned} V_{\text{P,obs}} &= \int (\Phi_{\mathcal{N}}(\ell) - p)^2 f_{\mathcal{N}}(\ell, \mu, V_{\text{P}}) d\ell + \int v(\ell) f_{\mathcal{N}}(\ell, \mu, V_{\text{P}}) d\ell, \\ &= \int \Phi_{\mathcal{N}}(\ell)^2 f_{\mathcal{N}}(\ell, \mu, V_{\text{P}}) d\ell - p^2 + \int \Phi_{\mathcal{N}}(\ell) f_{\mathcal{N}}(\ell, \mu, V_{\text{P}}) d\ell - \int \Phi_{\mathcal{N}}(\ell)^2 f_{\mathcal{N}}(\ell, \mu, V_{\text{P}}) d\ell, \\ &= p - p^2, \\ &= p(1 - p). \end{aligned} \quad (\text{S5})$$

This very simple analytical solution allows to easily compute  $V_{\text{P,obs}}$ . Of course, when fixed effects are included,  $p$  should be computed using Eq. S4.

**Consistency with Dempster & Lerner equation** Using Dempster and Lerner (1950) equation and the threshold model framework, one would compute the observed-scale heritability as:

$$h_{\text{obs, DL}}^2 = \frac{t^2}{p(1 - p)} \frac{V_{\text{A}}}{V_{\text{P}} + 1} \quad (\text{S6})$$

Note that the  $V_{\text{P}} + 1$  arise because of the addition of the so-called ‘‘link variance’’ (Nakagawa and Schielzeth, 2010). The term  $t$  is the probability density of a standard normal distribution evaluated at the  $p$ th quantile. Hence (standardising the latent distribution):

$$t = f_{\mathcal{N}}(\Phi^{-1}(p)) = f_{\mathcal{N}}\left(\frac{\mu}{\sqrt{V_{\text{P}} + 1}}\right) \quad (\text{S7})$$

On the other hand, using our framework, one would compute the observed heritability by computing  $\Psi$  as in Eq. 19, and combine it with Eqs. 8 & 18:

$$h_{\text{obs}}^2 = \frac{\Psi^2 V_A}{p(1-p)} \quad (\text{S8})$$

By comparing Eqs. S6&S8, one can see the identity holds if, and only if:

$$\Psi = \frac{t}{\sqrt{V_P + 1}} = f_{\mathcal{N}}(0, \mu, V_P + 1) \quad (\text{S9})$$

In order to prove this identity, let us compute the ratio between the two:

$$\begin{aligned} \Psi / f_{\mathcal{N}}(0, \mu, V_P + 1) &= \frac{\int f_{\mathcal{N}}(x) f_{\mathcal{N}}(x, \mu, V_P) dx}{f_{\mathcal{N}}(0, \mu, V_P + 1)} \\ &= \sqrt{\frac{V_P + 1}{V_P}} \frac{1}{\sqrt{2\pi}} \int \exp \left[ -\frac{1}{2} \left( x^2 + \frac{(x - \mu)^2}{V_P} - \frac{\mu^2}{V_P + 1} \right) \right] dx \\ &= \sqrt{\frac{V_P + 1}{V_P}} \frac{1}{\sqrt{2\pi}} \int \exp \left[ -\frac{1}{2} \left( \frac{(x + x V_P - \mu)^2}{V_P (V_P + 1)} \right) \right] dx \\ &= \sqrt{\frac{V_P + 1}{V_P}} \frac{1}{\sqrt{2\pi}} \int \exp \left[ -\frac{1}{2} \left( \frac{(x - (\mu / (V_P + 1)))^2}{V_P / (V_P + 1)} \right) \right] dx \\ &= \int f_{\mathcal{N}} \left( x, \frac{\mu}{V_P + 1}, \frac{V_P}{V_P + 1} \right) dx \\ &= 1 \end{aligned} \quad (\text{S10})$$

Note that, if fixed effects are included in the model,  $\Psi$  can be computed by averaging over them, as in Eq. S4:

$$\Psi = \frac{1}{N} \sum_i f_{\mathcal{N}}(0, \mu + (\mathbf{X}\hat{\mathbf{b}})_i, V_P + 1) \quad (\text{S11})$$

## B Proof for analytical solutions for Poisson traits

**Observed phenotypic mean** Here, we provide a derivation for the analytical expressions given for heritability in a Poisson GLMM. These are equivalent to those given in Foulley and Im (1993), and we give them in order to put the expressions in a form that is consistent with our notation. The observed phenotypic mean, hereafter noted  $\lambda$ , is the quantity (in absence of fixed effects):

$$\lambda = \int \exp(\ell) f_{\mathcal{N}}(\ell, \mu, V_P) d\ell = \exp(\mu + V_P/2) \quad (\text{S12})$$

after simplifications in Mathematica. Again, when fixed effects are included, it suffices to average over them:

$$\lambda = \frac{1}{N} \sum_i \exp(\mu + (\mathbf{X}\hat{\mathbf{b}})_i + V_P/2) = \frac{1}{N} \sum_i \lambda_i, \quad (\text{S13})$$

where  $\lambda_i$  is the observed mean conditional to  $(\mathbf{X}\hat{\mathbf{b}})_i$ .

**Expected-scale variance** In absence of fixed effects, the expected-scale variance is defined as follow (using Keonig's formula):

$$V_{P,\text{exp}} = \int \exp(\ell)^2 f_{\mathcal{N}}(\ell, \mu, V_P) d\ell - \lambda^2, \quad (\text{S14})$$

which simplifies into:

$$V_{P,\text{exp}} = \lambda^2 [\exp(V_P) - 1]. \quad (\text{S15})$$

When fixed effects, are included in the model, the formula does not simplify as much, because of the averaging:

$$V_{P,\text{exp}} = \exp(V_P) \frac{1}{N} \sum_i \exp(2\mu + 2(\mathbf{X}\hat{\mathbf{b}})_i + V_P) - \lambda^2 \quad (\text{S16})$$

Note that  $\lambda$  should be computed according to Eq. S15 in that case. Let us define the parameter  $\Lambda$  as

$$\Lambda = \frac{1}{N} \sum_i \exp(2\mu + 2(\mathbf{X}\hat{\mathbf{b}})_i + V_P) = \frac{1}{N} \sum_i \lambda_i^2, \quad (\text{S17})$$

so that  $V_{P,\text{exp}} = \Lambda \exp(V_P) - \lambda^2$ . The parameter  $\Lambda$  is the average of the squared values of  $\lambda_i$ . Unfortunately,  $\Lambda \neq \lambda^2$ , hence there is no further simplification.

**Distribution variance** Because the variance of a Poisson distribution is equal to the mean, the distribution variance reduces to  $\lambda$ :

$$V_{\text{dist}} = \int \exp(\ell) f_{\mathcal{N}}(\ell, \mu, V_{\text{P}}) d\ell = \lambda \quad (\text{S18})$$

When fixed effects are included in the model,  $\lambda$  should be computed as in Eq. S15.

**Observed-scale additive variance** In order to compute the observed-scale additive variance, we need the parameter  $\Psi$  defined in Eq. ?? in the main text. Again, because the derivative of an exponential is an exponential, the calculation reduces to  $\lambda$ :

$$\Psi = \int \exp(\ell) f_{\mathcal{N}}(\ell, \mu, V_{\text{P}}) d\ell = \lambda \quad (\text{S19})$$

Once again, when fixed effects are included in the model,  $\lambda$  should be computed as in Eq. S15. The observed-scale additive variance is then computed as  $\Psi^2 V_{\text{A}} = \lambda^2 V_{\text{A}}$ .

**Observed-scale heritability** In presence of fixed effects in the model, the heritability is consequently the “simple” following ratio:

$$h_{\text{obs}}^2 = \frac{\lambda^2 V_{\text{A}}}{\Lambda \exp(V_{\text{P}}) - \lambda^2 + \lambda} \quad (\text{S20})$$

**Negative-Binomial distribution** All the above results can be extended to the Negative-Binomial distribution, which, compared to the Poisson distribution, includes an overdispersion parameter (hereby noted  $\theta$ ). The new parameter  $\theta$  only affects the distribution variance such as:

$$h_{\text{obs}}^2 = \frac{\lambda^2 V_{\text{A}}}{\Lambda \exp(V_{\text{P}}) - \lambda^2 + \lambda + \exp(2(\mu + V_{\text{P}})) / \theta} \quad (\text{S21})$$

## C Calculation of the Price-Robertson identity

The Price-Robertson identity (Robertson, 1966; Price, 1970) is based on the covariance between the (latent) additive genetic values and the expected fitness. This covariance can be computed using Koenig’s formula for covariance:

$$\Delta\mu = \text{cov}(a, W_{\text{exp}}) = \text{E}[a \times W_{\text{exp}}] - \text{E}[a] \text{E}[W_{\text{exp}}] = \text{E}[a \times W_{\text{exp}}], \quad (\text{S22})$$

since, by definition,  $\text{E}[a] = 0$ . Hence we obtain the following complex calculation:

$$\text{cov}(a, W_{\text{exp}}) = \iint a(W_{\text{exp}}(\ell)) f(\ell|a) f(a) d\ell da = \iint a W_{\text{exp}}(\ell) f_{\mathcal{N}}(\ell, \mu + a, V_{\text{RE}} + V_{\text{O}}) f_{\mathcal{N}}(a, 0, V_{\text{A}}) d\ell da. \quad (\text{S23})$$

Double-integration can be difficult to solve, but we can simplify further the computation by noticing that:

$$\begin{aligned} \text{cov}(a, W_{\text{exp}}) &= \iint a W_{\text{exp}}(\ell) f_{\mathcal{N}}(\ell, \mu + a, V_{\text{RE}} + V_{\text{O}}) f_{\mathcal{N}}(a, 0, V_{\text{A}}) d\ell da, \\ &= \int a f_{\mathcal{N}}(a, 0, V_{\text{A}}) \int W_{\text{exp}}(\ell) f_{\mathcal{N}}(\ell, \mu + a, V_{\text{RE}} + V_{\text{O}}) d\ell da. \end{aligned} \quad (\text{S24})$$

Noting that

$$\text{E}[W_{\text{exp}}|a] = \int W_{\text{exp}}(\ell) f_{\mathcal{N}}(\ell, \mu + a, V_{\text{RE}} + V_{\text{O}}) d\ell, \quad (\text{S25})$$

we can simplify Eq. S24 into

$$\Delta\mu = \text{cov}(a, W_{\text{exp}}) = \int a \text{E}[W_{\text{exp}}|a] f_{\mathcal{N}}(a, 0, V_{\text{A}}) da. \quad (\text{S26})$$

## References

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