

Methods and results parrot mimicry

Methods

Statistical analysis

First we tried to understand what explained the presence of vocal mimicry across the parrot order. We ran ancestral state reconstruction with the function `contMap` from the package *phytools* [Revell, 2012]. We also ran a Bayesian model to test the strength of the phylogenetic model. We modelled the probability of a species being able to mimic and included a variance-covariance matrix with the covariance as a function of the phylogenetic distance, using the L2-norm. We used Stan to define the models [Gelman et al., 2015] and the package *cmdstanr* to fit [Gabry and Češnovar, 2022] with four chains, 1000 burn-in and 1000 sample iterations, and `adapt_delta = 0.95`. We used R-hat to monitor model convergence and report any deviation outside 0.99-1.01 in the results section.

$$\begin{aligned} M &\sim \text{binomial}(1, p) & M &= \text{mimicry or not} \\ \text{logit}(p) &\sim \text{MVnormal}(\mu, S) & p &= \text{probability of mimicry} \\ & & \mu &= \text{average log-odds mimicry} \\ & & S &= \text{variance co-variance matrix} \\ S_{ij} &= \eta^2 \exp(-\rho^2 P_{ij}^2) + \delta_{Pij} \sigma_P^2 & & \text{formula for L2 norm} \\ \eta^2 &\sim \text{exponential}(2) & P &= \text{normalised phylogenetic distance} \\ \rho^2 &\sim \text{exponential}(0.1) & \eta^2, \rho^2 &= \text{parameters for L2 norm} \end{aligned}$$

Next we modeled which covariates explained the presence of mimicry. To determine which covariates to include in each model we used causal graphs [Glymour et al., 2016, Wright, 1934], more specifically Directed Acyclic Graphs (DAGs) [Laubach et al., 2021]. Here one represents all assumed causal relationships between variables with arrows. Each arrow represents the direction of causality. From this back-door criterion informs which variables should be included as de-confounders [Glymour et al., 2016]. We were interested in the effect of longevity, relative brain size, sociality and body mass.

Longevity

We hypothesised that longevity could effect the presence of mimicry, since longer lived species would benefit more from learning new vocalisations throughout their lives. We included relative brain size, sociality and body mass as covariates. To control for potential shared evolutionary history we also included a varying effect for genus. Since our model contained missing values and we were interested in the effect of relative rather than absolute brain size we ran a structural equation model similar as suggested by Smeele [2022]. The main model was as follows:

model:

$$M \sim \text{binomial}(1, p)$$

$$\text{logit}(p) = \bar{\alpha} + \alpha_G + \alpha_S + \beta_L * L + \beta_{RB} * RB + \beta_B * B$$

$M = \text{mimicry or not}$
 $p = \text{probability of mimicry}$

priors:

$$\bar{\alpha} \sim \text{normal}(0, 1)$$

$$\alpha_G \sim \text{normal}(0, \sigma_G)$$

$$\sigma_G \sim \text{exponential}(2)$$

$$\alpha_S \sim \text{normal}(0, \sigma_S)$$

$$\sigma_S \sim \text{exponential}(2)$$

$$\beta_L \sim \text{normal}(0, 1)$$

$$\beta_{RB} \sim \text{normal}(0, 1)$$

$$\beta_B \sim \text{normal}(0, 1)$$

average log-odds mimicry
off-set for genus
between genera standard deviation
off-set for sociality
between sociality standard deviation
slope for longevity
slope for relative brain size
slope for body size

Missing values for longevity were imputed with the following sub-model:

model:

$$L \sim \text{normal}(\mu_L, \kappa_L)$$

$$\mu_L = \bar{\theta} + \theta_G + \zeta_{RB} * RB + \zeta_B * B$$

$L = \text{standardised life expectancy}$
 $\mu_L = \text{average life expectancy}$

priors:

$$\kappa_L \sim \text{exponential}(2)$$

$$\bar{\theta} \sim \text{normal}(0, 1)$$

$$\theta_G \sim \text{normal}(0, \kappa_G)$$

$$\kappa_G \sim \text{exponential}(2)$$

$$\zeta_{RB} \sim \text{normal}(0, 0.5)$$

$$\zeta_B \sim \text{normal}(0, 0.5)$$

standard deviation life expectancy
average life expectancy
off-set for genus
between genera standard deviation
slope for relative brain size
slope for body size

Relative brain size (RB) was computed and missing values were imputed with the following sub-model:

model:

$$\begin{aligned} Br &\sim \text{normal}(\mu_B, \phi_B) & Br &= \text{standardised brain size} \\ \mu_B &= \bar{\omega} + \omega_G + \gamma_B * B & \mu_B &= \text{average brain size} \\ PB &= \bar{\omega} + \gamma_B * B & PB &= \text{predicted brain size} \\ RB &= B - PB & RB &= \text{relative brain size} \end{aligned}$$

priors:

$$\begin{aligned} \phi_B &\sim \text{exponential}(2) & \text{standard deviation brain size} \\ \bar{\omega} &\sim \text{normal}(0, 1) & \text{average brain size} \\ \omega_G &\sim \text{normal}(0, \phi_G) & \text{off-set for genus} \\ \phi_G &\sim \text{exponential}(2) & \text{between genera standard deviation} \\ \gamma_B &\sim \text{normal}(0, 0.5) & \text{slope for body size} \end{aligned}$$

Relative brain size

We hypothesised that relative brain size could effect the presence of mimicry, since larger brains would allow a species to socially learn new vocalisations. We included sociality as covariate. The model structure was similar to that of longevity.

Sociality

We hypothesised that sociality could effect the presence of mimicry, since social species would benefit more and would have more opportunity to socially learn new vocalisations. We did not include any covariates. The model structure was similar to that of longevity.

Body size

We hypothesised that body size could effect the presence of mimicry, since larger species have a larger syrinx, which would make mimics more recognisable to a human observer. Furthermore, we expected larger species to be more often housed as single individuals, increasing the likelihood that they mimic vocalisations of their caretakers. We did not include any covariates. The model structure was similar to that of longevity.

The third goal of our study was to understand what drives the mimicry repertoire of a species. We were interested in the overall number of unique mimics and in the number of unique words produced by a species. For this we had multiple observations per species and therefore expanded the models to include a varying effect of species as well as of genus.

Longevity

We again hypothesised that longevity could effect the unique number of mimics, since longer lived species have more time to learn mimics. The main model was as follows:

model:

$$NM \sim \text{poison}(\exp(\lambda))$$

NM = number of mimics

$$\lambda = \bar{\alpha} + \alpha_G + \alpha_{Sp} + \alpha_S +$$

λ = average number mimics

$$\beta_L * L + \beta_{RB} * RB + \beta_B * B$$

priors:

$$\bar{\alpha} \sim \text{normal}(2, 2)$$

global average number mimics

$$\alpha_G \sim \text{normal}(0, \sigma_G)$$

off-set for genus

$$\sigma_G \sim \text{exponential}(2)$$

between genera standard deviation

$$\alpha_{So} \sim \text{normal}(0, \sigma_{So})$$

off-set for species

$$\sigma_{So} \sim \text{exponential}(2)$$

between species standard deviation

$$\alpha_S \sim \text{normal}(0, \sigma_S)$$

off-set for sociality

$$\sigma_S \sim \text{exponential}(2)$$

between sociality standard deviation

$$\beta_L \sim \text{normal}(0, 1)$$

slope for longevity

$$\beta_{RB} \sim \text{normal}(0, 1)$$

slope for relative brain size

$$\beta_B \sim \text{normal}(0, 1)$$

slope for body size

The sub-models to impute longevity and calculate and impute relative brain size were similar to the model of mimic presence. It should be noted that longevity and relative brain size were imputed at the species level, while the main model contained multiple observations for some species.

Relative brain size

We hypothesised that relative brain size could effect the number of unique mimics, since larger brains would allow a species to learn and remember more mimics. We included sociality as covariate. The model structure was similar to that of longevity.

Sociality

We hypothesised that sociality could effect the number of unique mimics, since social species would benefit more and would have more opportunity to socially learn new vocalisations. We did not include any covariates. The model structure was similar to that of longevity.

Body size

We hypothesised that body size could effect the number of unique mimics, since larger species have a larger syrinx, which would make mimics more recognisable to a human observer. Furthermore, we expected larger species to be more often housed as single individuals, increasing the likelihood that they mimic vocalisations of their caretakers. We did not include any covariates. The model structure was similar to that of longevity.

Results

We scored the vocal mimicry ability of 398 species (for the full distribution see Figure 1). 137 of showed at least one mimic. [Do we want to say something about the ancestral state reconstruction depicted in Figure 1?]

We ran four models to test the total effect of longevity, relative brain size, sociality and body size on the probability that a species can mimic. All variables had a positive total effect, although the effect of relative brain size was highly uncertain (see Figure 2).

We recorded the number of unique mimics that an individual produced for 843 individuals across 136 species. We ran four models to test the total effect of longevity, relative brain size, sociality and body size on the number of unique mimics that an individual produced in a video. Longevity had no effect, relative brain size had a highly uncertain effect, while sociality and body size had a small positive effect (see Figure 3).

We also tested the influence of the four variable on the unique number of words an individual produced in a video (see Figure 4). Longevity had a clear total effect. Relative brain size had no clear effect. Sociality and body size had a small and uncertain effect.

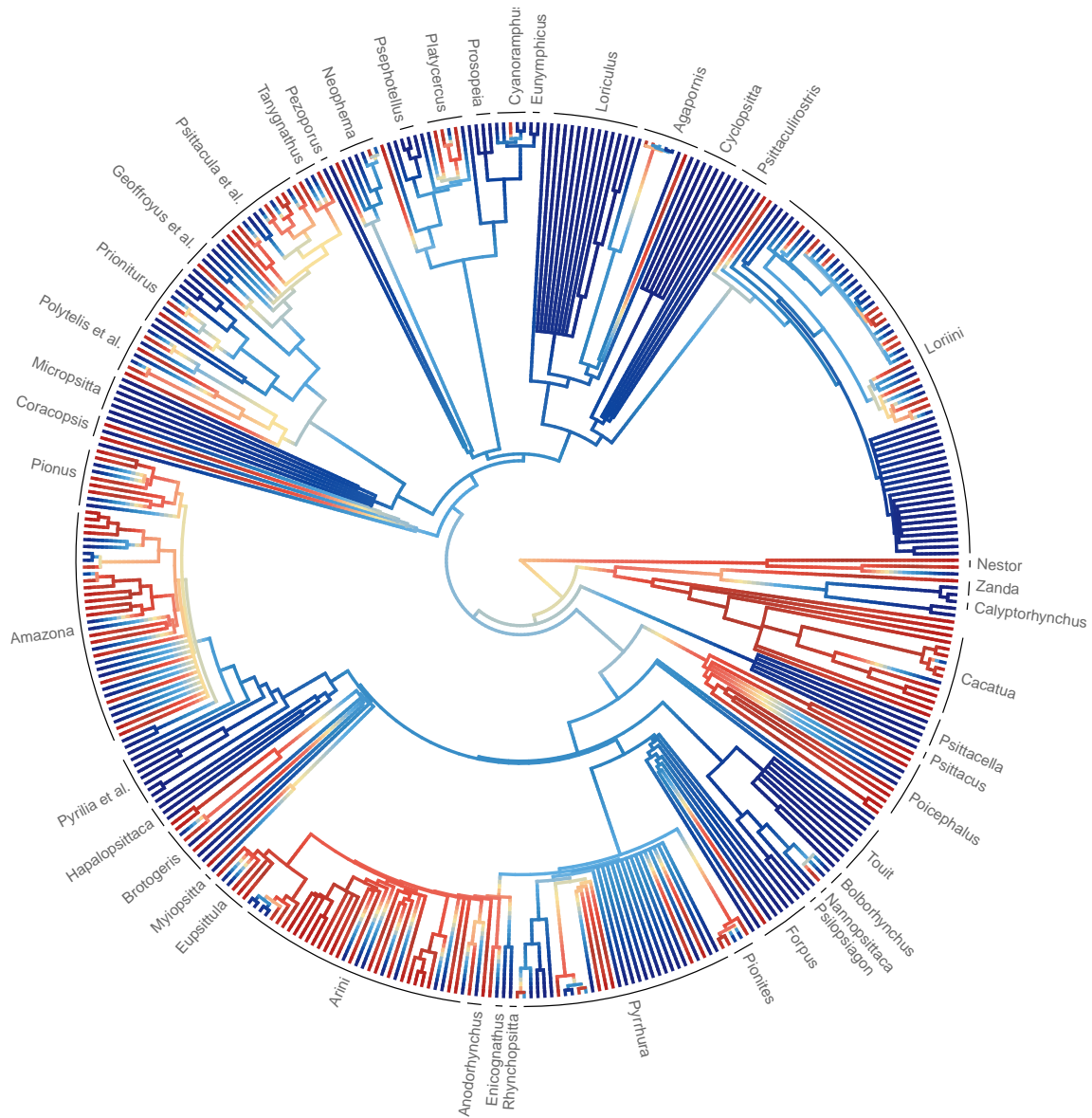


Figure 1: Phylogenetic tree of all parrots species for which vocal mimicry was assessed. Colours represent the ancestral state reconstruction of vocal mimicry ranging from blue = no vocal mimicry detected to red = vocal mimicry detected.

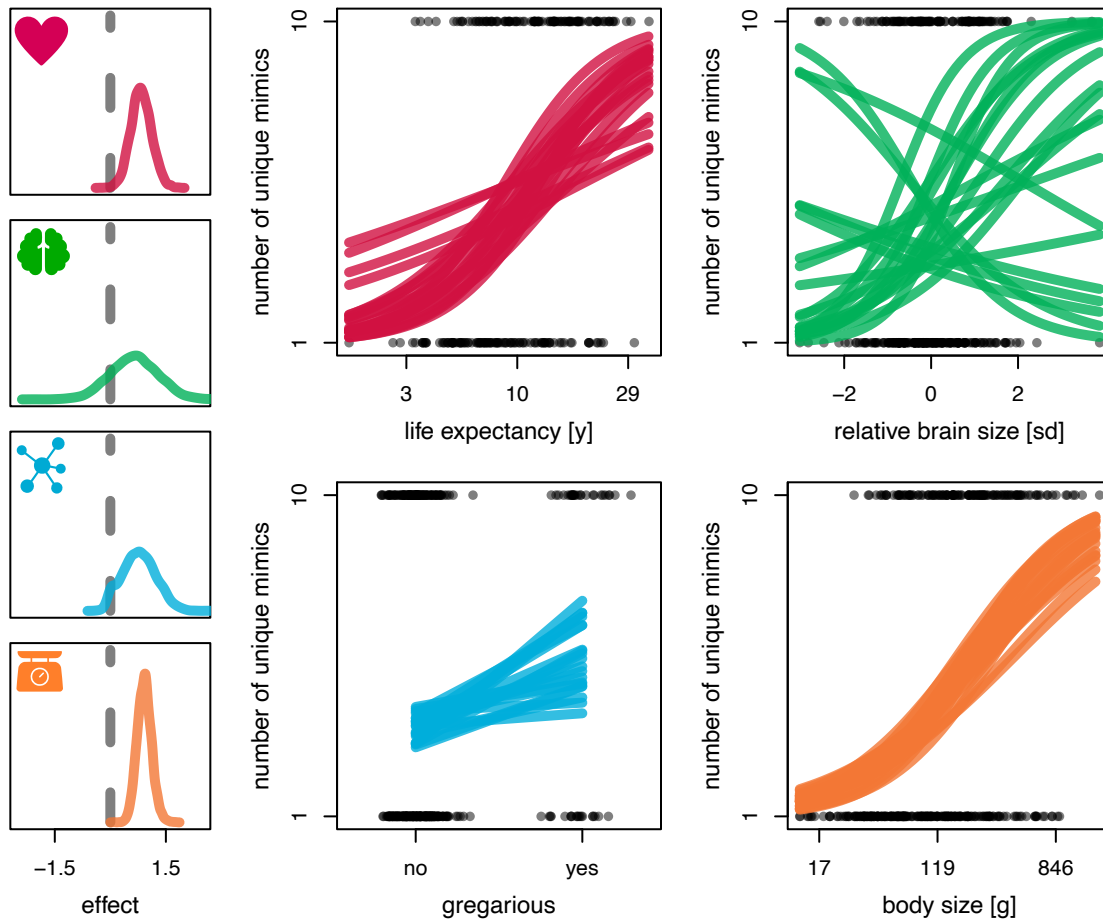


Figure 2: Variables influencing the probability of a species being able to mimic. Lefthand side: posterior densities of the effect of longevity (red), relative brain size (green), gregariousness (blue) and body size (orange). For gregariousness the contrast between a non-gregarious and a gregarious species is shown. For all other variables the slope is shown. Righthand side: scatterplots of the raw data (grey) and 20 posterior predictions (coloured lines) per variable.

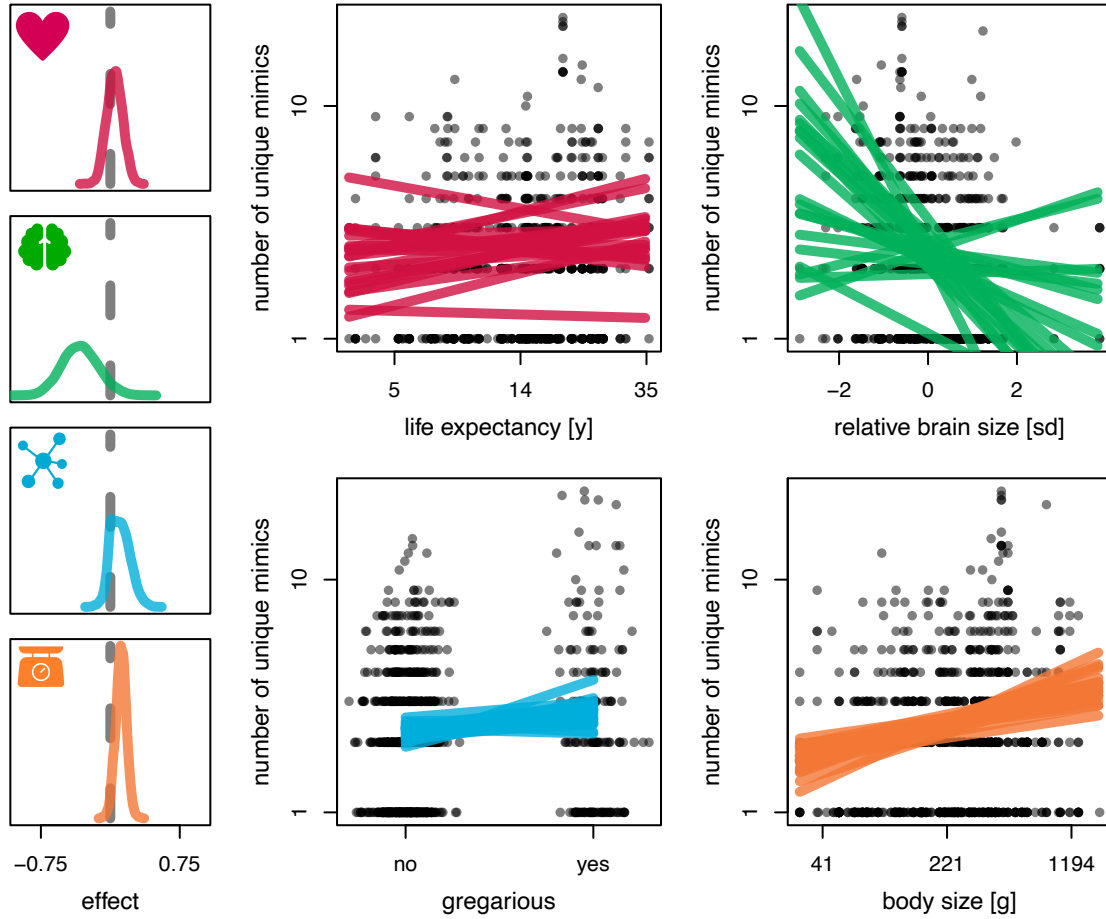


Figure 3: Variables influencing the number of mimics an individual produced in a video. Left-hand side: posterior densities of the effect of longevity (red), relative brain size (green), gregariousness (blue) and body size (orange). For gregariousness the contrast between a non-gregarious and a gregarious species is shown. For all other variables the slope is shown. Right-hand side: scatterplots of the raw data (grey) and 20 posterior predictions (coloured lines) per variable.

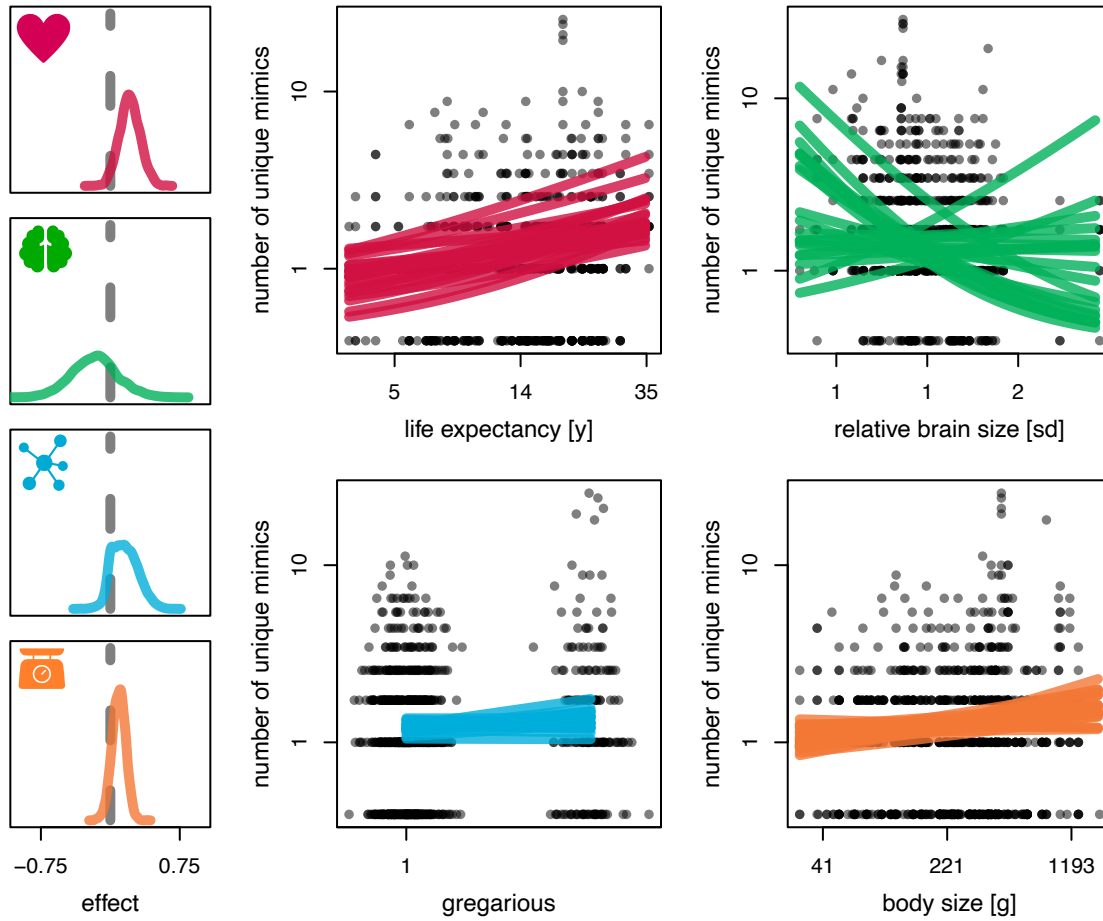


Figure 4: Variables influencing the number of words an individual produced in a video. Lefthand side: posterior densities of the effect of longevity (red), relative brain size (green), gregariousness (blue) and body size (orange). For gregariousness the contrast between a non-gregarious and a gregarious species is shown. For all other variables the slope is shown. Righthand side: scatterplots of the raw data (grey) and 20 posterior predictions (coloured lines) per variable.

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