
A hierarchical Bayesian approach to estimate endosymbiont infection rates

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2 ABSTRACT

3 Endosymbionts may play an important role in the evolution of the Insecta. Bacteria such as
4 *Wolbachia*, *Cardinium*, and *Rickettsia* are known to manipulate their host' reproduction to facilitate
5 their own. Indeed, there are many well know cases where *Wolbachia* (Alphaproteobacteria:
6 Rickettsiaceae) induces one of four manipulative phenotypes (cytoplasmic incompatibility, male
7 killing, feminization, and parthenogenesis). The scale of infection among species has been a
8 major subject of investigation, but this is not an easy endeavor and different approaches have
9 yielded different estimates. One aspect of this problem that may be underappreciated arises
10 when multiple yet independent samples are taken within a taxon. When independent samples
11 within a taxon are treated as levels of a hierarchy the problem is greatly simplified because error
12 propagates through the model in a realistic and intuitive manner. Here, we present a hierarchical
13 Bayesian approach to estimate infection frequency where multiple independent samples were
14 collected across multiple taxonomic levels. We apply this model to estimate the rates of infection
15 for *Wolbachia* in the Lepidoptera, and apply the model with a correction to account for phylogenetic
16 non-independence. In addition, we highlight the present body of knowledge regarding *Wolbachia*
17 and its effects with regards to the Lepidoptera. Our model estimates suggests that the rate of
18 endosymbiont infection in the order Lepidoptera is approximately 12%, which is much lower than
19 previously estimated. Given our limited knowledge regarding the phenotypes induced by these
20 endosymbionts, we urge caution when extrapolating the results of a positive assays.

21 **Keywords:** *Wolbachia*, Lepidoptera, modeling, butterfly, moth

1 INTRODUCTION

22 Bacterial endosymbionts have been known to inhabit insects for decades. These endosymbionts are
23 maternally transmitted to offspring through the cytoplasm of the egg. *Wolbachia* was the first of these
24 endosymbionts to be discovered when ? examined the adult ovaries and testes of *Culex pipiens* (hence
25 the specific epithet *Wolbachia pipiensis*) ?. Some years later, ? observed that male *C. pipiens* from
26 one geographic area may not successfully reproduce with females from a different area and reciprocal
27 crosses could produce similar results; this phenomenon was given the name *cytoplasmic incompatibility*.
28 A *Rickettsia*-like organism was determined to be the causative agent, which was later determined to be
29 *Wolbachia* (?).

30 Contemporary researchers detect the presence of *Wolbachia* via the polymerase chain reaction (PCR).
31 Today, any sample can be screened in a quick, easy, and relatively inexpensive manner (??), however, this
32 development is relatively recent. Prior to the advent of PCR, *Wolbachia* infection was only confirmed
33 through painstaking work that included electron microscopy and other microbiological techniques. Indeed,
34 these methods required such effort that they were employed once a researcher had an *a priori* reason
35 suspect the presence of the bacterium; we are aware of no cases in which exploratory assays for *Wolbachia*
36 were conducted prior to the appearance of PCR. It was under these circumstances that a researcher would
37 observe a likely reproductive manipulation phenotype (*male killing*, *feminization*, or *parthenogenesis*) and
38 then attribute it to *Wolbachia*.

39 Careful laboratory work is required to determine what (if any) phenotype is induced by an endosymbiont.
40 With the arrival of PCR and Sanger sequencing it became feasible to conduct exploratory investigations
41 for the presence of *Wolbachia*, though few studies conducted the experimental work to determine if any
42 reproductive manipulation was occurring. The effects of *Wolbachia* infection are complex and depend on
43 an interaction between the genomes of the endosymbiont and the host. For example, the phenotypic effects
44 of one strain of *Wolbachia* may be very different if moved into another host (??). Additionally, there may
45 be extensive genomic differences between closely related strains of *Wolbachia* (?). Though most famous
46 for its status as a "reproductive parasite," *Wolbachia* infections have been shown to induce no manipulation
47 at all (???). Without careful experimentation, it is not scientific to assume that *Wolbachia* will manipulate a
48 host simply because of a positive PCR assay.

49 The Lepidoptera (Arthropoda: Insecta) represent the best studied order of animals. Because of historic
50 interest in their physical beauty and their contemporary economic importance the literature is replete with
51 detailed knowledge regarding their distribution and life history. The Lepidoptera is a large Order containing
52 approximately 160,000 species in 124 families, which is approximately 13% all species currently known
53 ?. In addition to research focused on the Lepidoptera for pure biological reasons, the Lepidoptera are
54 also well represented on lists of endangered or threatened species (?). Researchers have tended to focus
55 on certain groups of Lepidoptera, such as the butterflies (e.g. Nymphalidae, Lycaenidae and Pieridae) or
56 groups of economically important pest species such as the Crambidae (which contains the Asiatic rice
57 borer *Chilo suppressalis* and Noctuidae (which contains the armyworms of the genus *Spodoptera*); this
58 results in a bias towards certain groups and leaves most of the remaining families understudied.

59 Experiments to determine if a naturally occurring manipulative phenotype exists have been conducted
60 for six species of Lepidoptera and report that *cytoplasmic incompatibility*, *male killing*, and *feminization*
61 occur (Table ??). We note that the report of *male killing* in *Ephestia kuhniella* is a result of *Wolbachia*
62 transfected from *Ostrinia scapulalis*. Because of the high level of interest in Lepidoptera research, there is

63 a considered enthusiasm for investigating the role that *Wolbachia* has played in its evolution. A vital first
64 step towards this goal is the estimation of *Wolbachia* infection rates in the Lepidoptera.

65 I think that this reads pretty well. I made some edits back when you were in Knoxville...

66 Here, we develop and employ a novel approach to the estimation of *Wolbachia* infection frequencies
67 across the Lepidoptera. Our model explicitly accounts for issues that arise with real world data, such
68 as those relating to estimating infection levels at different scales. For example, there may be multiple
69 observations of infection frequency collected from different populations within a species, often with
70 disparate sample sizes. We do not consider it appropriate for these samples to be completely pooled, as that
71 ignores population differences in infection frequency. Nor should observations within species be considered
72 independent, because of shared ancestry. Similarly, there may be single samples collected from many
73 different species within a family. In this case, individual sampling error should be accounted for when
74 estimating family level infection rates. Finally, we consider that there has been a bias towards studying
75 only a few families of the Lepidoptera. This uneven sampling can cause a few well-studied families to
76 drive estimates of overall infection frequency. Each of these concerns can be specifically considered and
77 accounted for with hierarchical Bayesian approaches that explicitly incorporate phylogenetic correlations.

78 In a hierarchical Bayesian approach, a compromise via partial pooling occurs. Lower levels of the
79 hierarchy inform higher levels of the hierarchy, and vice versa. When there is little information within a
80 grouping (e.g., species with few observations), those estimates are pulled strongly towards the among-group
81 mean. Conversely, parameter estimates for groups with a lot of information experience little shrinkage and
82 instead inform the estimates for groups with less information.

2 MATERIALS & METHODS

83 2.1 Motivating data and previous analyses

84 Both ? and ? used a likelihood-based approach to describe the distribution of *Wolbachia* infection across
85 arthropods and Lepidoptera, respectively. Both studies used beta-binomial models to estimate the mean
86 proportion of individuals infected within a given species (?). They used the same distribution to calculate
87 the incidence of infection as well, where incidence was the proportion of species infected above a threshold
88 frequency c (i.e., one infection in 1000 individuals, or 0.001; ?).

89 In the case of *Wolbachia*, insects screened for this bacterium may either be positive or not positive. It is
90 important to state that “not positive” is the appropriate state here because an infection could have been
91 missed for a number of reasons, including low density infections (?). However, for the sake of simplicity,
92 we will treat *Wolbachia* infection status as two mutually exclusive outcomes, (0 or 1; positive or not
93 positive). This makes the question of infection a binomial sampling problem. The issue is the way that
94 likelihood deals with error at each level, or rather how it does not. We will demonstrate this problem with
95 two examples. First, let us assume that 200 individuals of a species are assayed for *Wolbachia*, and 100 of
96 those tests are positive for infection. The mean estimate of infection is 0.5 and the 95% exact binomial
97 confidence interval is 0.43 ? 0.57. Next, let us say that two individuals from a species were assayed for
98 *Wolbachia*, and one tested positive. For this example, the proportion infected in this species is 0.5, however,
99 the 95% confidence interval is 0.01 ? 0.99. It is clear that there is uncertainty around each estimate and that
100 uncertainty varies with sample size. For this error to be properly incorporated into any estimate it must be
101 treated at each level of the analysis (each species), rather than at the level of the study.

102 **2.2 Data**

103 We used the data set synthesized by ?, which contains records from thousands of individual sampling
 104 efforts across the Arthropoda. These data were arranged such that each row represented one independent
 105 sampling event (though each row may contain data from multiple individuals sampled) and contained
 106 information on the family, genus, species, endosymbiont genus, number of individuals assayed, and
 107 number of positive individuals. We filtered these data such that they contained only *Wolbachia* assays of
 108 Lepidoptera. The filtered data set contained 1037 sampling events on 10860 individual Lepidoptera, of
 109 which 3607 screened positive for *Wolbachia* infection. We imported these data into the program R v3.2 (R
 110 Core Development Team) and there conducted all subsequent analyses. All data and code necessary to
 111 reproduce the analyses and figures in this paper are freely available on FigShare (DOI TBD: NB, the data
 112 will be accessioned to FigShare once the manuscript and code are in their final form).

113 To correct for any influence of the relatedness among families in our analysis, we used the Lepidoptera
 114 phylogeny of ?, which contained 115 of the 124 families in the order. The tree was pruned to remove
 115 duplicate families and those not present in the ? dataset. We then made the tree ultrametric following the
 116 penalized likelihood method of ? using tools in the *ape* package (?). To incorporate phylogenetic history
 117 into the Bayesian model, we used the pruned ultrametric tree to create a series of phylogenetic correlation
 118 matrices. We constructed one matrix in which we assumed that *Wolbachia* infection status was distributed
 119 according to Brownian Motion (BM), a model of trait evolution that assumes neighboring taxa share that
 120 trait due to common ancestry (?). We also constructed matrices that assumed trait evolution followed an
 121 Ornstein-Uhlenbeck (OU) process, which places constraints around which a character evolves (?). Relative
 122 to the BM, the OU model has two additional parameters: θ (the "optimal" value for a character), and α
 123 (the rate at which θ moves towards α) (?). The α value can range from 0 - 1; When α is 0 the model is
 124 effectively pure BM and becomes less so as α increases. We rescaled the Phylogeny using three alpha
 125 values to examine their impact: $\alpha = 0.1$ (similar to BM), $\alpha = 0.5$, and $\alpha = 0.9$ (very different than BM).

126 **2.3 Bayesian hierarchical models**

127 In contrast to ?, we adopted a hierarchical Bayesian approach to estimate the probability of infection
 128 prevalence within and among species of Lepidoptera using a subset of the data from ?. Each observation
 129 ($N = 1037$)—the number of *Wolbachia*-infected individuals—was nested within species ($S = 419$) and
 130 modeled as:

$$\text{infected}_{i,j} \sim \text{Binomial}(n_i, \theta_j). \quad (1)$$

131 where $i = 1, 2, \dots, 1037$ and $j = 1, 2, \dots, 419$. Here $\text{infected}_{i,j}$ indicates the number of infected
 132 individuals from the i th observation of the j th species, n_i is the total number of screened insects in
 133 observation i , and θ_j is the probability of infection for species j .

134 We then assumed the species-level probabilities of infection were normally-distributed with family-level
 135 means (μ_k) and standard deviations (σ_k) where $k = 1, 2, \dots, 28$ families. For computational efficiency, we
 136 used a non-centered parameterization of the normal (?). The normal distribution is unconstrained, but θ is
 137 bounded between zero and one. Therefore the species-level θ s were logit transformed such that

$$\text{logit}(\theta_j) \sim \text{Normal}(\mu_k, \sigma_k). \quad (2)$$

138 The mean (μ_k) describes the average probability of infection within a lepidopteran species family on the
 139 log-odds scale and can be back-transformed using the inverse-logit function.

The standard deviation (σ) measures how much variation in the probability of infection there is across species. If σ is small, then infection probabilities will be similar among species. Conversely, if σ is large, species-specific probabilities of infection will be more idiosyncratic. Data sparsity can be a problem in hierarchical models, especially for the estimation of scale parameters like variances. Because there were several species with few observations, we used a shrinkage prior (??) for the species-specific σ s:

$$\begin{aligned}\sigma_k &= t_{\nu}^+(0, \tau) \\ \tau &\sim t_{\nu}^+(0, 1)\end{aligned}\quad (3)$$

140 where t_3^+ is half-Student-t distribution with $\nu = 3$ degrees of freedom.

141 We modeled μ , the vector of log-odds infection probabilities for families using a multivariate normal
 142 distribution:

$$\begin{bmatrix} \mu_1 \\ \mu_2 \\ \vdots \\ \mu_k \end{bmatrix} = \text{MVNormal}(\gamma, \Sigma). \quad (4)$$

143 with the mean log-odds probability of infection across Lepidoptera (γ) and covariance matrix Σ . To account
 144 for phylogenetic non-independence among families, we constructed sigma as:

$$\Sigma = \boldsymbol{\eta} \boldsymbol{\Omega} \boldsymbol{\eta} \quad (5)$$

145 where $\boldsymbol{\eta}$ is a $k \times k$ diagonal matrix with the overall standard deviation on the diagonals and $\boldsymbol{\Omega}$ is a $k \times k$
 146 phylogenetic correlation matrix. We then put regularizing priors on both γ and $\boldsymbol{\eta}$:

$$\begin{aligned}\gamma &\sim \text{Normal}(0, 5) \\ \boldsymbol{\eta} &\sim t_{\nu}^+(0, 5)\end{aligned}\quad (6)$$

147 where again t_3^+ is half-Student-t distribution with $\nu = 3$ degrees of freedom.

148 Posterior probabilities for model parameters were estimated using Markov chain Monte Carlo (MCMC)
 149 sampling in the Stan programming language (?) via the RStan interface (?). For each model, four MCMC
 150 chains were used with 5,000 iterations each. The first 2,500 iterations for each chain were adaptive and thus
 151 discarded as warm-up. We used several diagnostic tests to confirm that each model had reached a stationary
 152 distribution including visual examination of MCMC chain history and calculation of effective sample
 153 size (ESS) and the Gelman-Rubin convergence diagnostic (\hat{R} ; ??). In particular, model convergence
 154 was assessed by inspecting the diagnostics of the log-posterior density. Model fit was also assessed by
 155 posterior predictive checks by simulating “new” data from the posterior distribution and plotting it against
 156 the original data.

157 We used WAIC (the widely applicable or Watanabe-Akaike information criterion; ??) to compare models
158 with different phylogenetic correlation matrices (e.g., Brownian motion vs. OU processes) using functions
159 in the loo package (?).

3 RESULTS

160 After filtering the ? data to contain only Lepidoptera that were screened for *Wolbachia* we retained 1037
161 independent sampling events with 411 unique species from 28 families, representing a total of 10860
162 individual assays. Of these, 3607 samples from 163 species and members of 19 families were scored PCR
163 positive for *Wolbachia*.

164 The \hat{R} diagnostic for all parameters (including the log-posterior density) was 1.0, indicating that each
165 model had reached a stationary posterior distribution. Visual assessment of the MCMC chain history
166 confirmed this. Additionally, the effective sample size for the log-posterior density was > 2000 for all
167 models. Predictive plots of the posterior medians of the simulated “new” observations regressed against
168 the original observations resulted in tight concordance, suggesting the models were doing a good job at
169 describing the data and providing a good fit.

170 All models, including those which contained phylogenetic correction, had similar WAIC scores with
171 standard errors that completely overlapped (Table ??). Therefore, each model was in the same “family”
172 of best models. Additionally, the results were almost identical across models, and all models predicted a
173 median infection frequency of $\sim 15\%$. Rather than consider each model separately, we created a consensus
174 model using model weighted averaging based on the Δ_{WAIC} scores (Table ??) to describe *Wolbachia*
175 infection frequency in the Lepidoptera.

176 Our estimate for the median *Wolbachia* infection frequency in the Lepidoptera was 12.1% (95%CI =
177 0.045 – 0.33; Figure ??). Estimates of median family-level infection frequencies varied considerably
178 with a positive association between sample size and credible interval (Figure ??). For example, the
179 Lycaenidae (878 specimens from 346 species) and Nymphalidae (4060 specimens from 236 species)
180 produced relatively tight distributions, while the families that had small sample sizes (e.g. Bombycidae,
181 Hedylidae, and Lasiocampidae) generated larger credible intervals to reflect uncertainty in the estimates.

4 DISCUSSION

182 Our model predicts a median *Wolbachia* infection rate for the Lepidoptera of approximately 12%, an
183 estimate that stands in considerable contrast to previously reported results. In a recent publication ?
184 estimated that approximately 80% of lepidopteran species were infected at non-negligible frequencies.
185 Similar to this estimate was that of ?, who reported *Wolbachia* incidence rates of $\sim 75\%$ for the order
186 Lepidoptera. Both of these studies employed similar approaches to estimate *Wolbachia* infection rates,
187 ? employed a beta-binomial model and ? employed both a beta and doubly-inflated beta, and also used
188 very similar data sets. Employing the same data set as ? we arrived at a much lower estimate of *Wolbachia*
189 infection rate than either previous study examining the Lepidoptera.

190 As with ?, we consider that there are three main sources of bias in the data set. From ? these biases are:
191 1) some species are represented by a single sample, 2) there is a taxonomic bias in the data, and 3) research
192 may be focused on groups with known *Wolbachia* infection (e.g. ?). We also consider a fourth type of bias
193 in the data, in that some families will be extensively sampled among a small number of different species,
194 which may bias the data towards a few members of an otherwise large family of Lepidoptera.

195 We suggest that our infection rate estimate is lower than previous research because our hierarchical
196 Bayesian model deals with these biases at each level and therefore may produce a more reliable estimate.

197 It is interesting to consider that our median infection frequency estimates for the Lepidoptera do not
198 significantly change when the model considers relatedness by incorporating phylogenetic information
199 (Figure ??). Additionally, the model WAIC scores were within 8 units of one another and their stand errors
200 completely overlapped, implying that the models did not significantly vary among (Table ??). We interpret
201 these results to indicate that our model is robust to differential sampling across the order Lepidoptera. We
202 consider our estimate for median *Wolbachia* infection rate for the Lepidoptera to be reliable and many
203 of the family level estimates similarly so. We consider the family level estimates that are generated by
204 large sample sizes to be reliable, but we must advise caution when interpreting some of these family
205 level estimates when they are generated using small sample sizes. In these cases where one sample has
206 been assayed for an entire family (Bombycidae, Callidulidae, Eupterotidae, Hedylidae, Lasiocampidae,
207 Pterophoridae, Uraniidae) the estimates presented in Figure ?? are driven by the grand mean for the
208 Lepidoptera.

209 There are a number of interesting implications if our results accurately reflect the real prevalence of
210 *Wolbachia* in the Lepidoptera. If the infection frequency for species is on the order of 12%, then perhaps
211 *Wolbachia* is not presently a major player in the evolution of this order. It follows that, if *Wolbachia*
212 infection frequency is relatively low in the Lepidoptera than its role in the evolution of the order may
213 not be as significant as with other groups (?). Evidence is accumulating that demonstrates *Wolbachia* is
214 not an obligate manipulator or a host' reproductive biology (???) and perhaps the paradigm needs to be
215 reevaluated. Indeed, ? demonstrated that reproductive manipulator microbes should evolve to minimize
216 harm to its host.

217 The assumption that *Wolbachia* always acts as a reproductive manipulator in incorrect (??) and one
218 must take significant care when extrapolating the results of a positive *Wolbachia* assay into to real world
219 effects. A *Wolbachia* infection can impart benefits to its host, for example the *wSuz* infection of *Drosophila*
220 *suzukii* confers resistance to certain viruses (?) and does not induce a manipulative phenotype (?). Thus,
221 simply because *Wolbachia* is detected does not and should not imply that the bacterium will be detrimental
222 to its host. Furthermore, our knowledge of *Wolbachia* as a reproductive manipulator in the Lepidoptera
223 is based on scant evidence. To the best of our knowledge, of the 163 species of Lepidoptera considered
224 positive for *Wolbachia*, only seven species from four families have been assayed for an induced phenotype
225 (Table ??). Reciprocal cross experiments are required to determine what (if any) effect *Wolbachia* has on
226 the reproduction of its host. Until these experiments are conducted for a particular system we urge extreme
227 caution when interpreting a positive PCR assay and hope that researchers will conduct the necessary
228 experiments to determine if a manipulative phenotype is even present in a particular system.

229 In many respects, scientific research with regards to *Wolbachia* is still in its "natural history" phase,
230 wherein we describe the distribution and effects of infection. Need to conclude here, must think on it.

231 ?

232 ?

233 ?

234 We conclude that the science of microbes in the Lepidoptera, especially with regards to the endosymbiont
235 *Wolbachia*, is still in its natural history phase wherein discovery is still largely in the descriptive phase, and
236 as such we urge caution when interpreting positive *Wolbachia* assays and extrapolating consequences.

CONFLICT OF INTEREST STATEMENT

237 The authors declare that the research was conducted in the absence of any commercial or financial
238 relationships that could be construed as a potential conflict of interest.

AUTHOR CONTRIBUTIONS

239 ZM and CH conceived of the experiment; ZM and CH conducted the analyses; ZM and CH wrote the
240 manuscript.

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245 Station for hosting us as we completed this manuscript.

SUPPLEMENTAL DATA

246 Supplementary Material should be uploaded separately on submission, if there are Supplementary Figures,
247 please include the caption in the same file as the figure. LaTeX Supplementary Material templates can be
248 found in the Frontiers LaTeX folder

FIGURES

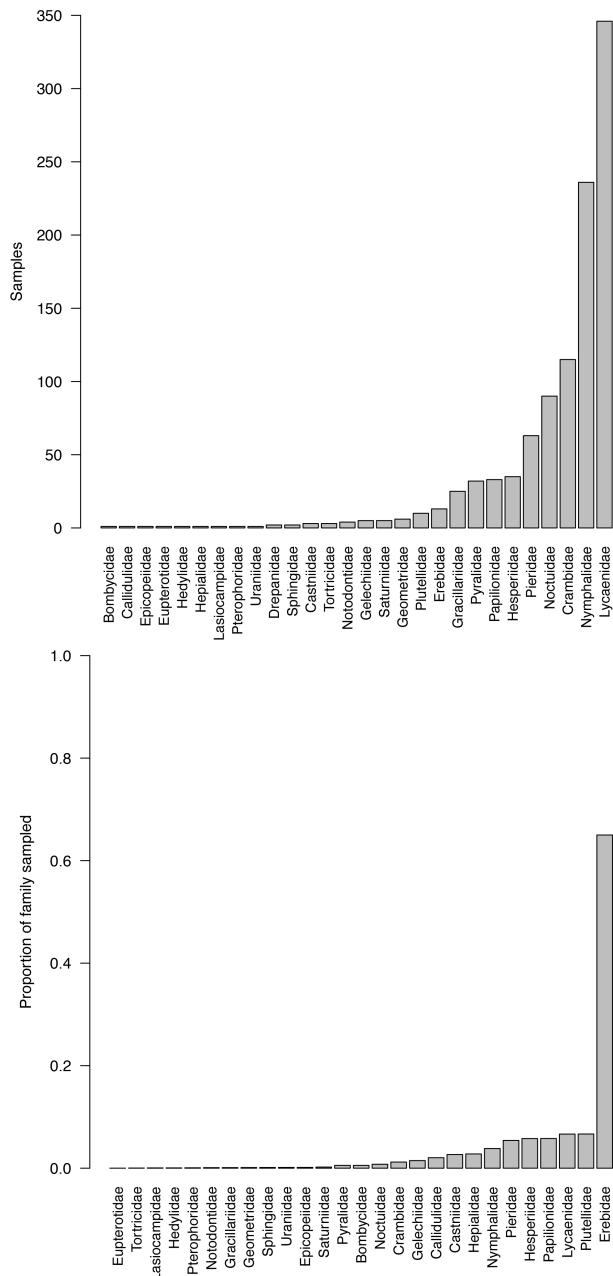


Figure 1. *Wolbachia* sampling by family for total number (**A**) and scaled by proportion of species sampled in each family (**B**).

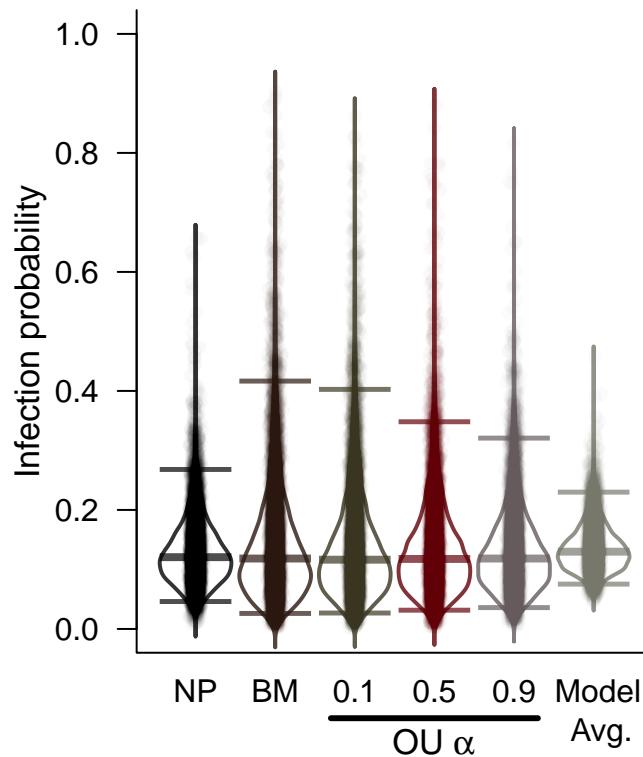


Figure 2. Posterior density plots for the average frequency of *Wolbachia* infection across Lepidoptera. Each posterior estimate is jittered and superimposed on the violins with transparency. Fatter regions of the violins indicate regions of higher posterior density, as do darker regions of jittered points. Horizontal bars indicate the median and upper and lower 95% Highest Density Interval (HDI). Models (L to R): NP = No Phylogenetic correction; BM = Brownian Motion; OU = Ornstein-Uhlenbeck with varying levels of α (0.1, 0.5, 0.9); Model Avg. = WAIC model weighted averaging.

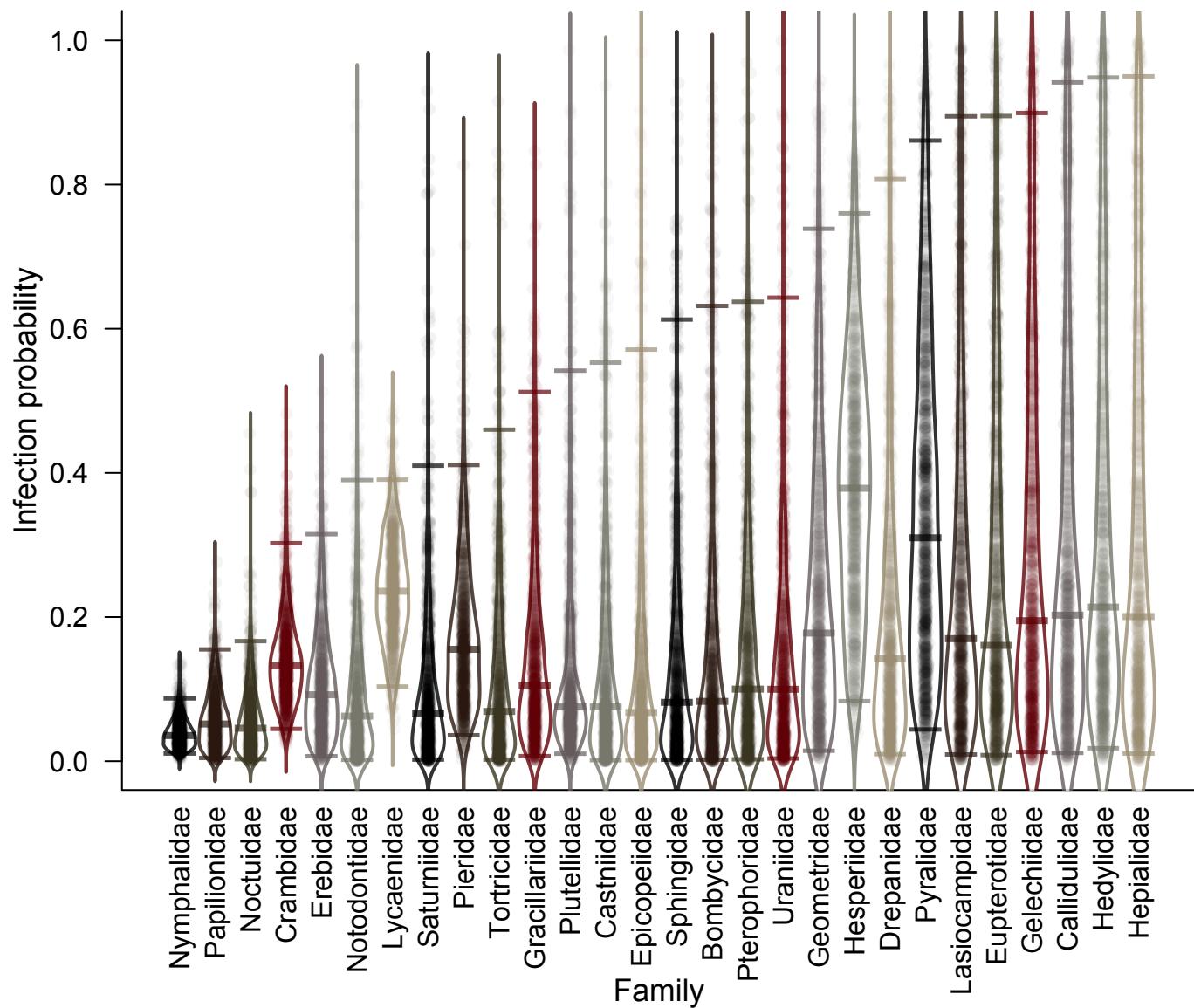


Figure 3. Posterior density plots for the average frequency of *Wolbachia* infection among 28 families of Lepidoptera. Each posterior estimate is jittered and superimposed on the violins with transparency. Fatter regions of the violins indicate regions of higher posterior density, as do darker regions of jittered points. Horizontal bars indicate the median and upper and lower 95% Highest Density Interval (HDI).

TABLES

Table 1. Published phenotypic effects of *Wolbachia* on Lepidoptera. Phenotype: MK = male killing, Fem = feminization, CI = cytoplasmic incompatibility. * = induced by transfection with *Wolbachia* strain from *O. scapulalis*.

Species	Family	Phenotype	Reference
<i>Acrea encedana</i>	Nymphalidae	MK	?
<i>Acraea encedon</i>	Nymphalidae	MK	?
<i>Ephesia kuehniella*</i>	Pyralidae	MK	?
<i>Eurema hecate</i>	Pieridae	CI	?
<i>Hypolimnas bolima</i>	Nymphalidae	MK	??
<i>Ostrinia scapulalis</i>	Crambidae	MK & Fem	?
<i>Ostrinia furnacalis</i>	Crambidae	Fem	?

Table 2. Models with different phylogenetic correlation structures ranked according to WAIC and their respective model weights. The no-phylogeny model had an identity matrix (ones on the diagonal and zeros on the off-diagonals) in place of a correlation matrix. Smaller WAIC values indicate better estimates. Δ_{waic} is the difference between each WAIC and the lowest WAIC value. SE_{waic} and SE_{Δ} are the standard errors for WAIC and Δ_{waic} respectively.

Model	WAIC	SE_{waic}	p_{waic}	Δ_{waic}	SE_{Δ}	weight
OU: $\alpha = 0.1$	3,458.7	318.1	245.2	0.0		0.79
OU: $\alpha = 0.5$	3,462.8	319.7	245.7	4.1	2.55	0.10
Brownian Motion	3,464.1	320.3	246.6	5.4	3.44	0.05
No Phylogeny	3,464.9	320.2	247.9	6.3	3.07	0.03
OU: $\alpha = 0.9$	3,465.9	320.1	247.1	7.2	3.13	0.02