

Avian diet and foraging ecology constrain foreign egg recognition and rejection

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Abstract

Egg rejection is a common and effective defense against avian brood parasitism in which the host either marginalizes or removes the parasitic egg or deserts the parasitized clutch. The ability to recognize and reject a parasitic egg depends on bill morphology, sensory systems, and cognition, all of which are also shaped by other selective processes such as foraging. This begs the question whether specific phenotypes associated with different foraging strategies and diets may constrain or facilitate egg recognition and rejection. Here, we propose a novel hypothesis that host species phenotypes related to foraging ecology and diet may impose morphological and visual sensory constraints on the evolution of egg recognition and rejection. We conducted a comparative analysis of the adult diets and egg rejection rates of 165 current host and non-host species. We found that species have significantly higher egg rejection rates when they (1) consume an omnivorous or animal and fruit dominated diet rather than seeds and grains, (2) forage arboreally rather than aerially or on the ground, or (3) possess relatively larger body sizes. Although correlational in nature, as predicted, these results suggest phenotypes related to specific diets and foraging ecologies may differentially constrain or facilitate evolution of host egg rejection defenses against avian brood parasitism.

Keywords

Egg rejection, foraging ecology, frugivory, granivory, host–parasite interactions, insectivory

Introduction

Obligate avian brood parasitism is a breeding strategy wherein a parasitic species lays its eggs into the nests of other species that provide parental care for the unrelated offspring.¹ Brood parasitism, by definition, is detrimental to the host's survival and reproductive effort, because parasitic chicks may require longer and more intensive provisioning than host broods, and host eggs or nestlings may be outcompeted, or otherwise eliminated, by the hatchling parasite.²

To reduce or forego many of these costs of avian brood parasitism, egg rejection is a common antiparasitic defense in which a host either removes the parasitic egg from the nest³ or deserts the parasitized nest.⁴ The likelihood of the hosts evolving egg rejection defense is predicted to be greater when the cost of raising brood parasite nestlings is higher.⁵ Yet, many host species do not reject foreign eggs, despite not only facing high costs of parasitism⁵ but also having their own eggs predicted to be readily perceived as visually different from brood parasite eggs,⁶ and also demonstrated physical capability of removing objects from the nest as large and heavy as foreign eggs.³ There are several adaptive hypotheses for why some host species have not evolved egg rejection, including the evolutionary equilibrium hypothesis, which suggests that the cost of breaking or mistakenly rejecting own eggs counterweighs the benefits of rejecting brood parasite eggs.⁷ A non-adaptive alternative

is the evolutionary lag hypothesis, which proposes that not enough time has passed since the onset of a coevolutionary host–brood parasite arms-race for the host to evolve egg rejection defenses.⁸

A novel, non-exclusive hypothesis in concordance with evolutionary lag for the absence of host egg rejection is that different host species' phenotypes may differentially constrain⁹ or facilitate the evolution of egg rejection over a period of time due to perceptual and physical limitations, despite the costs of raising unrelated offspring. Specifically, foreign egg recognition is only possible if the host is capable of perceiving brood parasite eggs as different from its own eggs, typically using visual cues.¹⁰ Furthermore, small host bill size or lower body mass may also limit the ability to remove a brood parasite egg from the nest.¹¹

How might species' phenotypes have been shaped in a manner that either constrains or facilitates the evolution of egg rejection? Foraging ecology and diet play predominant roles in the evolution of avian body size and cranial and bill

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morphology,^{12–16} visual perception and other sensory systems,^{17,18} and cognition decision rules.¹⁹ All of these morphological and neural traits may directly shape species' ability to recognize and/or remove a foreign egg from the nest.^{10,11} For example, granivorous bird species generally have bills that are wide in depth and short in length¹⁶; these may be unsuitable for piercing or grasping and removing foreign eggs.¹¹ Similarly, granivorous birds may have visual acuities that are poorer at the same distances than those of the visually guided insectivores which feed on highly mobile and/or often cryptic prey.^{20,21} In turn, frugivorous birds may be more sensitive and attuned to color differences than are granivorous birds, because chromatic differences are reliable long-distance cues for identifying ripe fruits.²² For example, trichromatic color vision is associated with frugivorous diets across primate species²³ and is also associated with greater ability to detect fruits at long distances, as well as a wider breadth of discriminable fruit colors, in trichromatic individuals of polymorphic tri/dichromatic capuchin populations.²⁴ Alternatively, achromatic features including shape and pattern contrast are likely more reliable than chromatic cues in identifying cryptic seeds on the ground for granivorous birds.²⁵ Therefore, we predict that insectivorous and frugivorous birds may possess visual sensory and perceptual traits better suited than those of granivorous birds for visually discriminating foreign eggs in their nests. The specific visual tasks and mechanisms leading to differences in foreign egg discrimination ability may include recognizing egg maculation pattern and color differences between own and foreign eggs.²⁶ The perception and processing of these cues, in turn, could be constrained by visual spatial resolution (i.e. acuity)²⁷ for a given species, and/or perceiving and attending to eggshell background color differences. Potential neurosensory mechanisms constraining color and spatiochromatic vision in birds include species-specific patterns of photoreceptor opsin and oil droplet tuning, relative photoreceptor densities, photoreceptor mosaic variation across the retina, and neural color opponency channels.^{28–32} Here, we test how foraging ecology and diet-related phenotypes may influence evolutionary trajectories of host egg rejection defenses using phylogenetic comparative methods.

Methods

Data

We collected data from published avian egg rejection studies for as many species as we could find (N=174), using “egg rejection” as keyword, then searched for the published diet data for the respective species and generated a final dataset of both egg rejection and categorized diet data, matched with a set of 100 phylogenetic hypotheses from BirdTree.org³³ for N=165 species (supplementary data). For each species, our complete dataset included the following: weighted average egg rejection rate (weighted by study experiment sample sizes), average body mass (g),³⁴ average tarsus length, and bill length, width, and depth (mm).³⁵ Additional categories included diet and forage zone,³⁴ the associated obligate avian brood parasite taxon (*Cuculidae*

and *Molothrus*), and whether the species is a known current host of its associated brood parasite, that is, “host status.”^{36,37} Diet categories included the following: “frugivore” (N=3), “granivore” (N=13), “insectivore” (N=54), “insectivore/frugivore” (N=37), “insectivore/granivore” (N=27), “nectarivore/insectivore” (N=5), and “omnivore” (N=26) and were assigned using food and feeding descriptions from the *Handbook of the Birds of the World* (HBW).³⁴ Omnivores were assigned as species with food and feeding descriptions including the term “omnivorous.” For further analyses, where diet category was included as a predictor, strict frugivores (N=3) and nectarivores/insectivores (N=4) were excluded due to low species numbers. We also included foraging zone as one of the three categories: “ground,” “arboreal,” or “aerial.” Categories followed the foraging classification system of the Cornell Lab of Ornithology online bird guide (<https://www.allaboutbirds.org/guide/>). Foraging behavior descriptions from HBW were also used: “ground” was indicated if a species' description included “forages mainly on ground,” “arboreal” was indicated if the description included “forages in canopy/trees/shrubs,” and “aerial” was indicated if the description included “forages while in flight; forages × meters above ground.”

Discrete assigned diet categories may not adequately capture relevant degrees of variation among proportions of food types within avian diets. Therefore, we also collected published quantitative measurements of species' diets for N=96 species. We collected percent diet composition for adults, mainly measured as percent stomach content volume (N=81), percent fecal content volume (N=8), or stomach or fecal content frequency proportion (N=7). We separated major food sources into three major categories: animal, fruit, and seed. Finally, we followed Olson et al.³⁸ and used a 7-point scoring system to bin animal, seed, and fruit diet proportions for all species. Scoring was necessary to reduce the potential measurement error due to between-study differences in diet categorization, and to include verbal descriptions of species' diets in cases where precise numerical estimates were not provided. Scores for animal, fruit, and seed diet were assigned by the percent contributed to species' entire diets: 0%–1% scored as 1, 1.1%–16% scored as 2, 16.8%–33% scored as 3, 33.4%–50% scored as 4, 50.1%–66.7% scored as 5, 66.8%–83.4% scored as 6, and 83.5%–100% scored as 7. For each of these 96 species, our dataset again included the following: weighted average egg rejection rate (weighted by study sample sizes), average body mass (g), average wing chord (mm), average tarsus length (mm), average length of bill culmen (mm), average bill width and depth (mm),³⁵ animal diet, seed diet, fruit diet, forage zone, associated brood parasite taxon, and whether the species is a known current host of a brood parasite.

We included both species considered to be evolutionarily “current hosts” or “non-hosts” (sensu)³⁹ in all analyses together because the focal interest of this study is to directly examine the relationship of the ability to recognize and reject foreign eggs from the nest with foraging ecology phenotypes, and not with the influence of host–brood parasite coevolution systems per se.

Table 1. Principal component scores from phylogenetic PCA on morphological measurements of N=96 species.

	PC1-size	PC2-tarsus versus bill shape	PC3-bill length	PC4	PC5	PC6
Bill length	-0.76	0.24	0.56	-0.21	-0.03	0.04
Bill width	-0.74	-0.54	0.09	0.17	-0.35	-0.01
Bill depth	-0.82	-0.33	0.05	0.17	0.43	0.04
Body mass	-0.94	0.12	-0.16	-0.13	0.03	-0.25
Wing chord	-0.86	-0.01	-0.36	-0.33	-0.05	0.16
Tarsus length	-0.74	0.52	-0.11	0.40	-0.08	0.06
Standard deviation	1.99	0.86	0.70	0.63	0.57	0.30
Proportion of variance	0.66	0.12	0.08	0.07	0.05	0.02
Cumulative proportion	0.66	0.78	0.87	0.93	0.98	1
PCA model λ	0.87					

PCA: principal component analysis.

Comparative phylogenetic analyses

For the full dataset, we ran five separate Bayesian *MCMCglmm*⁴⁰ predicting egg rejection rates for N=165 species. We ran all *MCMCglmm* over 100 phylogenies using the *mulTree* package⁴¹ in R,⁴² using a weakly informative parameter expanded prior ($V=1$, $v=1$, prior mean $\alpha \cdot \mu=0$, $\alpha \cdot V=10$)^{3,43,44} setting the number of MCMC generations to 4,000,000, the thinning interval to 1500, and the burn in period to 100,000. Models were run in parallel over seven chains to obtain at ≥ 1500 samples per chain. Model convergence between model chains was assessed using the Gelman–Rubin statistic, the potential scale reduction factor (PSR), and all were models required to have a PSR below 1.1.⁴⁵

We ran five separate models with the full dataset (N=165): (1) testing the influence of species' foraging zone (*aerial*, *arboreal*, or *ground*), (2) testing for differences among associated brood parasite taxon and host status (*Cuculidae* vs *Molothrus*, current *host* vs *non-host*, and their interaction), (3) testing the influence of species' categorized diet phenotypes with *insectivores*, the most common diet phenotype, set as the comparison group (i.e. *insectivore/fruitivore*, *insectivore/granivore*, *granivore*, and *omnivore* vs *insectivore*), and two separate models testing the influence of categorized diet phenotypes in (4) current *Molothrus* hosts only (N=56), and (5) current *Cuculidae* hosts only (N=53). \log_{10} -transformed body mass was also included as a predictor in all models, except for the host status model, to account for the influence of species' body sizes. For the current hosts only diet category models, strict *granivores* were excluded due to low species numbers in the separate samples of *Molothrus* (N=3 *granivores*) and *Cuculidae* (no *granivores*) hosts.

For the reduced dataset of N=96 species, we first performed two separate phylogenetic principal component analyses (pPCAs).⁴⁶ First, we ran a morphology-based pPCA on \log_{10} -transformed measurements of body mass, bill length, wing chord, tarsus length, bill length, bill width, and bill depth. The first three components explained 87% of all variation in species' bill and body morphologies, and we named these components based on interpreted

Table 2. Principal component scores from phylogenetic PCA on animal, fruit, and seed diet scores of N=96 species.

	PC1-animal versus seed	PC2-fruit versus seed	PC3- omnivory
Animals	0.98	0.16	0.11
Fruits	-0.40	-0.90	0.15
Seeds	-0.77	0.62	0.12
Standard deviation	0.40	0.29	0.06
Proportion of variance	0.64	0.34	0.02
Cumulative proportion	0.64	0.98	1.00
PCA model λ	0.85		

PCA: principal component analysis.

axes of their loadings: PC1-size, PC2-tarsus versus bill width, and PC3-bill length (see Table 1). Second, we ran a separate diet-based pPCA using animal, seed, and fruit diet scores. We included all three components from this pPCA and named them as follows: PC1-animal versus seed diet, PC2-fruit versus seed diet (multiplied by -1 to interpret positive values as higher proportion of fruit diet), and PC3-omnivory (see Table 2). Phylogenetic signal was high for both the morphology (Pagel's $\lambda=0.87$) and diet pPCA (Pagel's $\lambda=0.85$), indicating that closely related species share highly similar morphologies and diets. We ran a single *MCMCglmm* predicting species' egg rejection rates with predictors of PC1-size, PC2-tarsus versus bill width, PC3-bill length, PC1-animal versus seed, PC2-fruit versus seed, and PC3-omnivory, over 100 phylogenies using the same model prior and parameters as described above. Egg rejection rates were mean-centered and scaled to 1 standard deviation from the mean for all models.

Results

All *MCMCglmm* passed convergence (PSR < 1.1) and produced ≥ 1500 posterior estimates per each predictor from 100 iterations of each model, where each iteration was run with a separate phylogenetic hypothesis. Bayesian inference provides an estimate of the probability of a hypothesis given the data.⁴⁷ We present the posterior mode and 95%

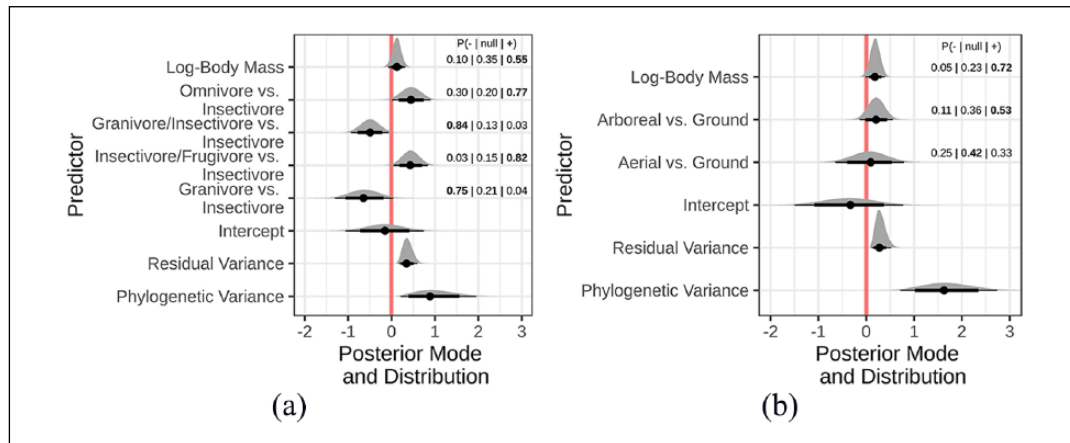


Figure 1. Full dataset models testing the influence of (a) diet and (b) forage zone on egg rejection rates in $N = 165$ species. Posterior modes and distributions, their 95% highest density intervals (HDIs) (thin line), 80% HDIs (thick line), and posterior probabilities of having either negative, null, or positive effects on egg rejection rates are presented. The highest posterior probability for the existence of an effect of a predictor having negative, null, or positive relationship with egg rejection rates are indicated in bold. No posterior probabilities are provided for the intercept, model residual variance, or phylogenetic variance because the intercept is centered toward zero and the variances are positive-only values.

highest density interval (HDI) of each model predictor as a point estimate and distribution of effect size to infer both the magnitude and direction of a predictor's effect on avian egg rejection responses. Our degree of certainty in the true existence of an effect for a predictor is expressed as a posterior probability for a negative, null, or positive influence of a predictor on avian egg rejection (for an overview of Bayesian inference, see Ellison⁴⁷). Model predictors' posterior modes and 95% HDIs were calculated from the highest density region of combined posterior distributions across all 100 model iterations using the *tidybayes* package in R.⁴⁸ Posterior probabilities of effects of predictors⁴⁷ having negative ($P-$), null ($P0$, probability of predictor having an effect within an interval around zero), and positive ($P+$) effects on egg rejection rates were calculated using the *BayesCombo* package in R.⁴⁹

Categorized diet predicting egg rejection

For the full dataset models including all species associated with both *Molothrus* and *Cuculidae* brood parasites (both current host and non-host species included), the omnivorous (posterior mode=0.45, 95% HDI=[0, 0.90], $P-|P0|P+=0.04|0.2|0.77$; Figure 1(a)) and insectivore/frugivore species (posterior mode=0.44, 95% HDI=[0.05, 0.84], $P-|P0|P+=0.03|0.15|0.82$; Figure 1(a)) have higher egg rejection rates in comparison with mainly insectivorous species, while granivorous species have relatively lower egg rejection rates (granivore posterior mode=-0.63, 95% HDI=[-1.30, 0.05], $P-|P0|P+=0.75|0.21|0.04$; granivore/insectivore posterior mode=-0.49, 95% HDI=[-0.93, -0.06], $P-|P0|P+=0.84|0.13|0.02$; Figure 1(a)). Higher body mass is associated with higher egg rejection rates (\log_{10} -body mass posterior mode=0.12, 95% HDI=[-0.08, 0.32], $P-|P0|P+=0.1|0.35|0.55$; Figure 1(a)). Residual variance posterior mode=0.35 and 95% HDI=[0.16, 0.59] (Figure 1(a)). Phylogenetic variance posterior mode=0.90 and 95% HDI=[0.20, 1.95] (Figure 1(a)).

Forage zone predicting egg rejection

In comparison with ground foraging species, arboreal foragers have marginally higher egg rejection rates (posterior mode=0.21, 95% HDI=[-0.14, 0.56], $P-|P0|P+=0.11|0.36|0.53$; Figure 1(b)), whereas no discernable pattern was found in the comparison between aerial and ground foragers (posterior mode=0.09, 95% HDI=[-0.65, 0.79], $P-|P0|P+=0.25|0.42|0.33$; Figure 1(b)). In concordance with the diet category models, higher body mass is associated with higher egg rejection rates (\log_{10} -body mass posterior mode=0.18, 95% HDI=[-0.01, 0.39], $P-|P0|P+=0.05|0.23|0.72$; Figure 1(b)). Residual variance posterior mode=0.27 and 95% HDI=[0.11, 0.52] (Figure 1(b)). Phylogenetic variance posterior mode=1.64 and 95% HDI=[0.71, 2.74] (Figure 1(b)).

Associated brood parasite taxon and host status predicting egg rejection

Overall, species associated with *Cuculidae* brood parasites have lower egg rejection rates than species associated with *Molothrus* brood parasites (posterior mode=-0.86, 95% HDI=[-1.44, -0.28], $P-|P0|P+=0.97|0.03|0$; Figure 2(a)), and current host species have lower egg rejection rates than non-host species (posterior mode=-0.46, 95% HDI=[-0.90, -0.01], $P-|P0|P+=0.79|0.18|0.03$; Figure 2(a)). Accordingly, because both associated brood parasite taxon and host/non-host status are combined to predict a substantial amount of variation in species' egg rejection rates (interaction between associated brood parasite taxon and host status in posterior mode=1.18, 95% HDI=[0.55, 1.80], $P-|P0|P+=0|0|1$; Figure 2(a)), we ran separate diet category models predicting egg rejection rates of current hosts of *Cuculidae* brood parasites and current hosts of *Molothrus* brood parasites. Residual variance posterior mode=0.28 and 95% HDI=[0.12, 0.48] (Figure 2(a)). Phylogenetic variance posterior mode=1.42 and 95% HDI=[0.67, 2.46] (Figure 2(a)).

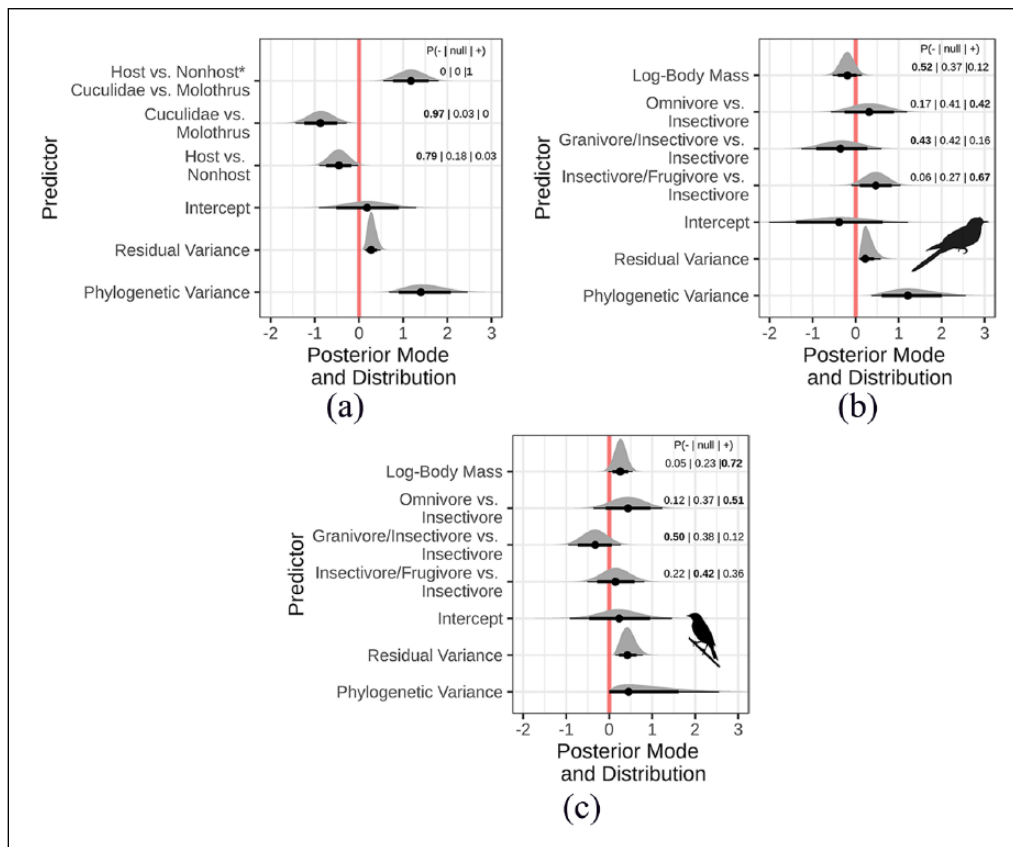


Figure 2. Full dataset model testing the influence of (a) associated brood parasite taxon and host status in N = 165 species. Reduced dataset models testing the influence of diet on egg rejection rates in current hosts of (b) *Cuculidae* (N = 53) and (c) *Molothrus* (N = 56) brood parasites. Posterior modes and distributions, their 95% highest density intervals (HDI; thin line), 80% HDI (thick line), and posterior probabilities of having either negative, null, or positive effects on egg rejection rates are presented. The highest posterior probability for the existence of an effect of a predictor having negative, null, or positive relationship with egg rejection rates are indicated in bold. No posterior probabilities are provided for the intercept, model residual variance, or phylogenetic variance because the intercept is centered toward zero and the variances are positive-only values.

Categorized diet predicting egg rejection in *Cuculidae* or *Molothrus* hosts

In *Cuculidae* hosts (N = 53 species), larger body mass is marginally associated with lower egg rejection rates (\log_{10} -body mass posterior mode = -0.19, 95% HDI = [-0.53, 0.02], $P_{-|P0|P+}$ = 0.52|0.37|0.12; Figure 2(b)). In comparison with mainly insectivorous hosts, omnivores have marginally higher egg rejection rates (posterior mode = 0.32, 95% HDI = [-0.57, 1.20], $P_{-|P0|P+}$ = 0.17|0.41|0.42; Figure 2(b)) and insectivore/frugivores have credibly higher egg rejection rates (posterior mode = 0.47, 95% HDI = [-0.10, 1.04], $P_{-|P0|P+}$ = 0.06|0.27|0.67; Figure 2(b)). Granivore/insectivore *Cuculidae* hosts have marginally lower egg rejection rates than insectivore hosts (posterior mode = -0.33, 95% HDI = [-1.26, 0.60], $P_{-|P0|P+}$ = 0.43|0.41|0.16; Figure 2(b)). Residual variance posterior mode = 0.23, 95% HDI = [0.08, 0.58] (Figure 2(b)). Phylogenetic variance posterior mode = 1.21, 95% HDI = [0.36, 2.55] (Figure 2(b)).

In *Molothrus* hosts (N = 56 species), larger body mass is associated with higher egg rejection rates (\log_{10} -body mass posterior mode = 0.26, 95% HDI = [-0.02, 0.54], $P_{-|P0|P+}$ = 0.05|0.23|0.72; Figure 2(c)). In comparison with mainly insectivorous hosts, omnivores have marginally

higher egg rejection rates (posterior mode = 0.44, 95% HDI = [-0.37, 1.24], $P_{-|P0|P+}$ = 0.12|0.37|0.51; Figure 2(c)) but insectivore/frugivore diet type does not credibly predict egg rejection rates (posterior mode = 0.15, 95% HDI = [-0.51, 0.82], $P_{-|P0|P+}$ = 0.22|0.42|0.36; Figure 2(c)). Granivore/insectivore *Molothrus* hosts have marginally lower egg rejection rates than insectivore hosts (posterior mode = -0.33, 95% HDI = [-0.95, 0.27], $P_{-|P0|P+}$ = 0.50|0.38|0.12; Figure 2(c)). Residual variance posterior mode = 0.42 and 95% HDI = [0.14, 0.78] (Figure 2(c)). Phylogenetic variance posterior mode = 0.46 and 95% HDI = [-0.02, 2.54] (Figure 2(c)).

Quantitative diet and egg rejection

In a subset of N = 96 species for which we collected quantitative measures of diet, we found PC3-omnivory to be negatively associated with egg rejection rates (posterior mode = -0.39, 95% HDI = [-0.87, 0.10], $P_{-|P0|P+}$ = 0.65|0.28|0.07; Figure 3), greater frugivory (PC2-fruit vs seed* - 1: posterior mode = 0.20, 95% HDI = [-0.31, -0.10], $P_{-|P0|P+}$ = 0|0|1; Figure 3), and consumption of animals (PC1-animal vs seed: posterior mode = 0.08, 95% HDI = [0, 0.16], $P_{-|P0|P+}$ = 0.03|0.18|0.78; Figure 3) to be positively associated with higher egg rejection rates. For

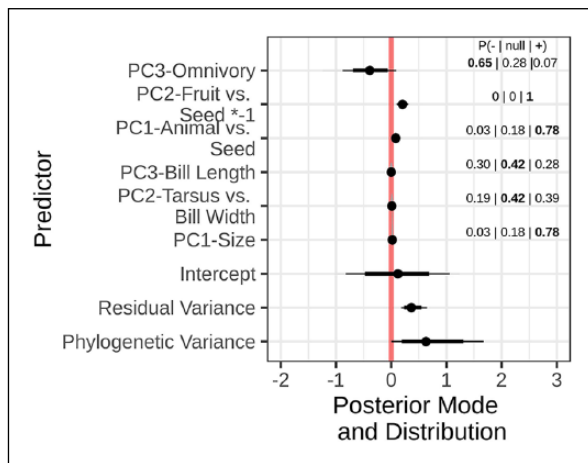


Figure 3. Reduced dataset model testing the effect of quantitatively measured diets on egg rejection rates in $N=96$ species. Diet data collected from published studies where physical contents of consumed items were observed (i.e. stomach or fecal content). Posterior modes and distributions, their 95% highest density intervals (HDI; thin line), 80% HDIs (thick line), and posterior probabilities of having either negative, null, or positive effects on egg rejection rates are presented. The highest posterior probability for the existence of an effect of a predictor having negative, null, or positive relationship with egg rejection rates are indicated in bold. No posterior probabilities are provided for the intercept, model residual variance, or phylogenetic variance because the intercept is centered toward zero and the variances are positive-only values.

morphological predictors, larger species have higher egg rejection rates (PC1-size* - 1: posterior mode=0.02, 95% HDI=[0.03, 0], $P_{-|P0|P+}=0.01|0.06|0.93$; Figure 3) but PC2-tarsus versus bill width was not predictive of species' egg rejection rates (posterior mode=0.01, 95% HDI=[-0.02, 0.05], $P_{-|P0|P+}=0.19|0.42|0.39$; Figure 3). Bill length, as captured by our pPCA, seems to have no direct association with egg rejection rates (PC3-bill length: posterior mode=0, 95% HDI=[-0.05, 0.05], $P_{-|P0|P+}=0.3|0.42|0.29$; Figure 3). Residual variance posterior mode=0.38 and 95% HDI=[0.18, 0.66] (Figure 3). Phylogenetic variance posterior mode=0.64 and 95% HDI=[0.01, 1.73] (Figure 3).

Discussion

Across all bird species sampled, omnivorous and frugivorous diet rather than insectivorous diet, insectivorous diet rather than granivorous diet, arboreal rather than aerial or ground foraging, and relatively larger body mass were predictive of more frequent rejection of foreign eggs (Figure 1(a) and (b)). When accounting for the influence of host-brood parasite coevolutionary relationships, directional effects of all diet types on egg rejection rates were similar across both *Cuculidae* and *Molothrus* hosts (Figure 2(b) and (c)), albeit to a less pronounced degree than when testing effects of diets on egg rejection in a combined dataset of both current hosts and non-hosts associated with both brood parasite taxa (Figure 1(a)). Furthermore, these patterns between diet types and egg rejection rates remain consistent when diets are measured as quantitative diet

proportions of diet categories, rather than discrete categorical traits (Figure 3). The exception to consistency between qualitative and quantitative models is our “omnivorous” diet principal component score (i.e. PC3-omnivory, which explains 2% of the variation in diet in the reduced $N=96$ dataset), as omnivorous diet was associated with higher egg rejection rates in the full qualitative models and lower egg rejection rates in the reduced quantitative model. However, this principal component likely did not adequately characterize omnivorous diet and overall variation in diet because it was limited to broad categories of animal, fruit, and seed consumption alone while disregarding finer-scale food types within these categories. Finally, as with all comparative studies, the patterns detected here are correlational in nature,⁵⁰ and future studies should explore both assumptions and direct causal linkages between foraging ecology, visual system traits, and egg rejection cues in avian obligate brood parasite host species.

An alternative explanation for the patterns we found between diet types and egg rejection rates may be that species with diets considered to be unsuitable for brood parasite nestlings are far less likely to be parasitized, and therefore do not need to evolve egg rejection defenses in the first place.^{51,52} Specifically, in our analyses, diet unsuitability may explain the lack of egg rejection defenses that is found in highly granivorous species (Figures 1(a), 2(b), 2(c)). Indeed, a recent study found that common cuckoos *Cuculus canorus* prefer to parasitize host species that feed their nestlings insects over those that do not,⁵³ and *Molothrus* cowbird nestlings are known to depend on animal protein to survive and fledge from host nests.⁵⁴ However, contrary to this scenario, many potential host species consume mainly insects and feed highly insectivorous diets to their young during the breeding season and switch to eating mainly seeds and grains in the nonbreeding season, and we account for these species in our analyses (i.e. “granivore/insectivore”). In addition, adult and nestling diets can differ from one another during the breeding season. For example, adult starlings (*Sturnus vulgaris*) consume large amounts of fruit in the fall and winter, but their nestlings are not provisioned with fruits even when fruits are available during the nestling feeding period.⁵⁵ Our data are drawn from descriptions and data available for adult birds only and, thus, they likely do not provide an accurate representation of diets fed to nestlings. Accordingly, our results are conservative in that they more directly apply to the foraging ecology hypothesis regarding adult phenotypes.

Our results suggest that, in addition to known effects of the degree of brood parasite egg mimicry⁶ and the potential costs associated with being parasitized,⁵ phenotypic traits known to be associated with different foraging strategies and diets (e.g. visual sensory systems and morphology) may differentially constrain or facilitate the evolution of host species' ability to recognize and reject a foreign egg by its color,¹⁰ maculation pattern, and/or shape and size. For example, visually guided insectivorous birds possess visual fields predicted to be better suited for eye-beak coordination than birds that consume immobile food,²⁰ and better eye-beak coordination may confer greater ability to

physically remove a foreign egg from the nest. In addition, frugivory is facilitated by use of chromatic cues and object-background contrasts,^{22,23} and the range of ripe fruits which can be consumed is limited by minimum bill gape-width,⁵⁶ which may also carry over into discrimination between colors of own versus foreign eggs, as well as the ability to grasp and remove an egg from the nest.¹¹ Body mass and eye size are highly and positively correlated in birds,^{18,57} and larger eye sizes are associated with higher visual acuities.^{58,59} Accordingly, the positive relationships we found between greater body mass and egg rejection rates may indicate that greater visual acuity, along with larger body and bill size, confers greater sensory and motor abilities to recognize and reject foreign eggs. For example, higher visual acuity may allow for greater ability to visually resolve egg patterning (e.g. egg spotting and scrawling) from a wider range of viewing distances. Importantly, although we found evidence that certain diet and foraging ecology-related phenotypes influence foreign egg recognition and rejection rates, our study does not directly examine specific sensory and physical mechanisms that may influence egg rejection defenses. Therefore, we suggest future comparative and experimental studies use our results as a guideline for examining suites of morphological, sensory, or cognitive traits that may form a mechanism explaining the patterns we found here (e.g. complete bill morphometrics, visual acuities, photoreceptor densities, color discrimination ability, etc.).

In summary, we provide exploratory support for the hypothesis that foraging ecology and diet may affect the evolutionary trajectory of egg rejection defenses in avian brood parasite hosts. Specifically, we predict current and future hosts of avian brood parasites that do not currently exhibit egg rejection defenses to more readily evolve egg rejection if they are omnivorous or frugivorous rather than insectivorous, insectivorous rather than granivorous, forage arboreally rather than in the air or on the ground, and have a relatively large body size.

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Author contributions

A.B.L. and M.E.H. conceived the study, A.B.L. collected and analyzed the data, and both authors wrote and edited the final draft of the manuscript.

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Supplemental material

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