



Clutch size and the rejection of parasitic eggs: a comparative test of the maternal investment hypothesis

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Abstract

Obligate brood parasitic birds lay their eggs in the nests of other species, reducing the host's own reproductive output. To circumvent these fitness costs, many—but not all—host species have evolved the ability to recognize and reject brood parasitic eggs. What factors constrain egg rejection, and why do host species vary in their likelihood of rejection? Previous comparative studies have found that egg rejection rates covary with several biotic factors (including larger body size, smaller relative brain size, and more northerly breeding latitudes), but much behavioral variation in the occurrence of egg rejection remains unexplained. In this study, we test a corollary of the maternal investment hypothesis, by assessing whether species with higher clutch sizes are more likely to eliminate parasitic eggs. We examined two published data sets comprising over 200 unique bird species, controlling for phylogeny and other known interspecific correlates of egg rejection rates. Contrary to the prediction, we found no evidence for a positive relationship between clutch size and egg rejection rate. Rather, our analyses suggest a weak but consistent negative relationship between absolute and relative metrics of clutch size versus egg rejection rate across species. These results are instead consistent with two previously proposed alternative hypotheses: that egg rejection is constrained by a trade-off between maternal investment and anti-parasitic defenses, possibly mediated by endocrine mechanisms linked to parental care, and/or that cognitive decision rules facilitate the detection of dissimilar eggs in smaller clutches.

Keywords Endocrine trade-off · Egg rejection · Host-parasite coevolution · Relative clutch size

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Introduction

Parental care is costly due to the time and energy needed to provision dependent young, the reduced effort spent on self-maintenance by the parent, and the increased predation risk experienced by both parent and offspring (Clutton-Brock 1991). Some bird, fish, and insect lineages escape these costs of parental investment through obligate brood parasitism (Pollock et al. 2021). These parasites lay their eggs in other species' nests, forcing the foster parents to raise the unrelated offspring unless they can detect the deception and reject the parasitic egg(s) or young (Soler 2017). Brood parasitism is one of the most ecologically unique yet evolutionarily important behaviors across the avian phylogeny (Kruger 2007): although only ~100 (1%) bird species are obligate brood parasites, including the familiar common cuckoo (*Cuculus canorus*) in Eurasia and the various cowbirds (*Molothrus* spp.) in the Americas, they affect over 1700 (~17%) of all avian species that serve as potential hosts (Antonson et al. 2020).

Caring for unrelated parasitic young is clearly maladaptive, especially when they evict or outcompete the host's own offspring (Moskat et al. 2017); yet many host species have not evolved any detectable anti-parasitic defense behaviors, such as the recognition and rejection of foreign eggs from the nest (Peer and Sealy 2004; Medina and Langmore 2015). Other host lineages have engaged in a co-evolutionary arms race with parasites and possess sophisticated egg recognition and elimination mechanisms (Safran and Vitousek 2008). However, individual variation exists even in these "egg rejector" species: although most individuals remove parasitic eggs from the clutch, some foster parents continue to accept the parasitic egg as their own (Rothstein 1982; Davies and Brooke 1989; Cruz et al. 2008).

Why, and how, does such variability persist within and between host species in their ability to recognize and reject foreign eggs? Previous evolutionary hypotheses to explain variation in rejection behaviors by hosts have considered the time elapsed between the onset of parasitism and the evolution of anti-parasitic defenses (e.g., the evolutionary lag model) or the relative ratio of the benefits of rejection to its costs (e.g., the evolutionary equilibrium model) (Rothstein 1990; Manna et al. 2017). At the proximate level, comparative analyses have demonstrated that egg rejection rates are positively correlated with several ecological, morphological, neurosensory, and biogeographical factors (including larger body size, larger eye size, smaller relative brain size, and more northerly breeding latitudes) (e.g., Peer and Sealy 2004; Ausprey and Hauber 2021; Aviles and Garamszegi 2007; Medina and Langmore 2015). Overall, however, tests of these non-mutually exclusive hypotheses have found inconsistent support, and additional variation continues to be explained by other factors when tested (e.g., foraging ecology: Luro and Hauber 2020).

In this paper, we take a multivariate approach to simultaneously account for multiple geographic, behavioral, morphological, and life history correlates of egg rejection. We used, as well as combined, two previously published data sets comprising over 200 species that have been documented as hosts of brood parasites, (Medina and Langmore 2015; Luro and Hauber 2020) and examined several potential predictors of egg rejection. Specifically, we tested the maternal investment hypothesis, which proposes that potential host species with larger clutch investments should derive greater benefits from rejecting parasitic eggs, hence protecting their increased reproductive efforts. This hypothesis has been taken specifically to predict a positive correlation between clutch size metrics and egg rejection rates (*sensu* Hauber et al. 2020) but it should also apply to other proxies of clutch investment, including absolute or female body-size corrected relative clutch volume or weight.

By contrast, negative correlations between clutch size and egg rejection rate would be consistent with the alternative hypotheses that physiological and/or cognitive mechanisms generate prohibitive trade-offs between egg acceptance (of the host's own eggs) and egg rejection (of parasitic eggs; sensu Abolins-Abols and Hauber 2018). Such trade-offs could occur, for example, if the same endocrine pathways that promote parental care behaviors also reduce the likelihood of egg rejection (e.g., corticosterone: Abolins-Abols and Hauber 2020a, and prolactin: Ruiz-Raya et al. 2021), or if the detection of foreign eggs is more perceptually challenging when the host's own clutch is large (e.g., Weber's rule: Akre and Johnsen 2014; Abolins-Abols and Hauber 2020b; Dixit et al. 2021). Critically, both of these alternative hypotheses predict that increased host clutch size should constrain, rather than favor, egg rejection behaviors.

Relatively few previous studies have used comparative methods to test for correlations between clutch size and egg rejection behavior, and these have primarily supported the alternative hypotheses predicting that increased maternal investment constrains rejection rate (e.g., Medina and Langmore 2015). In the first intraspecific test of the maternal investment hypothesis, Hauber et al. (2020) found no support for the predicted positive correlation between clutch size and probability of egg rejection in female American Robins (*Turdus migratorius*). However, in this same study, robin mothers with higher levels of corticosterone precursors in their egg yolks were more likely to reject foreign model eggs, consistent with a negative physiological trade-off between parental care and egg rejection (Hauber et al. 2020).

An endocrine linkage has also been supported directly by two recent experimental studies that manipulated levels of corticosterone (which suppresses parental care) and prolactin (which elevates it). Abolins-Abols and Hauber (2020a) found that experimental inhibition of corticosterone in female robins was associated with decreased egg rejection, whereas Ruiz-Raya et al. (2021) found that experimental inhibition of prolactin in female Eurasian Blackbirds (*Turdus merula*) was associated with increased egg rejection. Across species, the comparative analysis of Medina and Langmore (2015) also found qualitative support for a negative correlation between parental investment (clutch size) and egg rejection rate, although the correlation was not statistically significant ($p = 0.07$).

Here we use published comparative data sets from the literature (Medina and Langmore 2015; Luro and Hauber 2020) to generate multiple sets of host species, and we apply phylogenetically controlled analyses to test for hypothesized interspecific correlations between absolute and relative metrics of clutch size versus egg rejection probability while simultaneously accounting for other factors that have been demonstrated to influence rejection behavior, including parasitic eviction or nest-sharing behaviors and host body size, breeding latitude, and relative brain size.

Methods

We downloaded two open-access comparative data sets on egg rejection and body size from the published literature (Medina and Langmore 2015: $n = 198$ species, and Luro and Hauber 2020: $n = 165$ species). We then supplemented each of these data sets with our focal predictors of egg rejection behavior as well as factors previously identified in the literature, including mean breeding latitude and mean clutch size (from the Birds of the World species accounts; Billerman et al. 2020), relative brain size (sensu Aviles and Garamszegi 2007; data from Fristoe et al. 2017), body mass (Hauber 2003; Medina and

Langmore 2015), phylogenetic placement (BirdTree; Jetz et al. 2012), and parasite type (“evictor,” in which the parasitic nestling evicts the host nestling(s), or “nest-sharer,” in which the parasitic nestling competes with host nestlings in the brood; Antonson et al. 2020; our data available on Figshare.com, see Data Availability statement). To focus on current host-parasitism interactions, we analyzed only documented host species from each dataset [Medina and Langmore (2015) also includes non-parasitic species not known to be hosts, but we excluded these from our analysis].

We probed the two data sets in several ways, each time using phylogenetic controls. First, we assessed the role of clutch size, body mass, breeding latitude, and parasite type on egg rejection rates for each full data set separately. Second, we trimmed the data to remove species that always accept (0% rejection) or never accept (100% rejection) to better accommodate our linear models, resulting in reduced species lists for each data set (Medina and Langmore 2015: $n=81$ species, Luro and Hauber 2020: $n=86$ species), and repeated the above comparative analyses for each data set separately.

Third, we combined the original two data sets (resulting in 221 unique species; again, data available on Figshare.com, see Data Availability statement) of which we were able to obtain published data on relative brain size for 130 species (see above). We then conducted two additional comparative analyses on this combined species list: first, we assessed the directional impact of clutch size, body mass, breeding latitude, parasite type, and relative brain size on egg rejection rates. Second, we calculated a relative metric of clutch size (clutch size/adult body mass) for each species and assessed the directional impact of this relative clutch size, breeding latitude, parasite type, and relative brain size on egg rejection rate. By calculating a relative clutch size metric as a function of body mass, we accounted for both the known covariation of smaller clutch sizes with greater body sizes and larger egg sizes with increasing body sizes in birds (Saether 1989).

We used a phylogenetic generalized least squares approach (PGLS, Pinheiro et al. 2015) to identify associations between each candidate predictor and egg rejection rate. All of the numerical predictors were centered and scaled by subtracting the mean and dividing by the standard deviation before entering them into the models. We ranked and ordered each model in all model sets by calculating their Akaike Information Criterion (AIC) values corrected for small sample sizes (AICc) and report the best supported models $\Delta\text{AIC} (\leq 2)$ identified in the model selection process (Mazerolle 2017). We also conducted model-averaging of these same top models to generate estimates of beta values and the importance factors (i.e., the sum of the models’ weights that contain the predictor) for the predictors in each subset of models (Burnham and Anderson 2002).

We obtained 10,000 randomly generated phylogenetic trees from BirdTree based on the source of “Hackett All Species”. We created a consensus tree for the analyses by applying the maximum clade credibility method (Rambaut et al. 2018; Suchard et al. 2018), whose consensus tree had the maximum sum of posterior clade probabilities in the Bayesian sample (TreeAnnotator v1.8.3; Rambaut and Drummond 2016). All statistical analyses were conducted in R v4.0.3 (R Core Team 2020).

Results

When analyzing the two datasets separately, both of the two full species lists and the two reduced species lists produced AIC models that included models in the top set ($\Delta\text{AICc} \leq 2$; Supplementary Table S1) where clutch size was negatively correlated with

egg rejection rates. As found previously, both body mass and latitude positively predicted egg rejection rates across these top models (Table 1). Finally, egg rejection rates were lower in hosts parasitized by nest-sharers, relative to those parasitized by evictors.

The two analyses of the combined unique-species dataset with relative brain sizes available (n = 130) resulted in three competing top models for the absolute clutch size analysis ($\Delta AICc \leq 2$), one of which was the full model (Supplementary Data). Predictors of egg rejection rates in this model included body mass (positive), latitude (positive), relative brain size (negative), clutch size (negative), and parasite type (hosts of nest-sharers having lower values than hosts of evictors; Table 1). The best-fitted model with the lowest AICc score also included four of these terms with the same direction of correlation (again including a negative effect of clutch size on egg rejection rate) but excluded latitude (Fig. 1A). In turn, the analyses resulted in two competing top models for the relative clutch size analysis, one of which was again the full model (Supplementary Data). Predictors in the best model did not include latitude, whereas relative brain size (negative), relative clutch size (negative), and parasite type (hosts of nest-sharers having lower values than hosts of evictors) had the same signs as in the analysis for the absolute clutch size, but relative clutch size was a consistently significant predictor (both $p < 0.03$) in each of these two models (Fig. 1B; Supplementary Data).

Table 1 Averaged parameters ordered by their importance values for the different datasets in the best subsets ($\Delta AICc < 2$) of phylogenetically controlled models

Variables	Original datasets			Variables	Reduced datasets		
	β	SE	Importance		β	SE	Importance
Luro and Hauber (2020): n = 165 species				n = 86 species			
Parasite type	-19.518	6.3357	1	Body mass	4.038	2.2267	0.6736
Body mass	4.0695	2.3032	0.6064	Evictor versus sharer	-2.707	2.3132	0.3426
Latitude	1.1845	1.2625	0.349	Latitude	0.507	0.8054	0.2407
Clutch size	-0.5827	0.954	0.2936	Clutch size	-0.019	0.6912	0.2041
Medina and Langmore (2015): n = 175 species				n = 81 species			
Body mass	5.88	4.409	1	Body mass	5.499	4.1651	1
Parasite type	-23.808	9.167	1	Parasite type	-16.92	7.5446	0.8798
Clutch size	-1.5503	1.4397	0.3763	Clutch size	-0.842	1.097	0.2651
Latitude	1.081	1.3954	0.3166	Latitude	-0.178	0.9385	0.2221
Combined dataset: n = 221 species				n = 110 species			
Body mass	2.8222	3.5772	1	Body mass	6.955	3.1271	1
Parasite type	-17.811	5.4021	1	Parasite type	-9.028	4.4323	0.7108
Latitude	0.9284	1.0726	0.3357	Clutch size	-0.636	0.89	0.2832
Clutch size	-0.676	0.8766	0.3174	Latitude	0.373	0.7952	0.2525
Abs. clutch size with rel. brain size: n = 130				Rel. clutch size with rel. brain size: n = 130			
Brain size	-8.9006	4.9912	1	Brain size	-7.856	4.7612	1
Parasite type	-14.285	6.7325	0.8258	Relative clutch size	-9.227	4.0965	0.8731
Clutch size	-4.2139	2.4462	0.6287	Parasite type	-16.05	4.0965	0.8713
Latitude	-0.0544	0.9221	0.1993	Latitude	-0.099	0.804	0.1871

Our focal predictor in this study is in bold

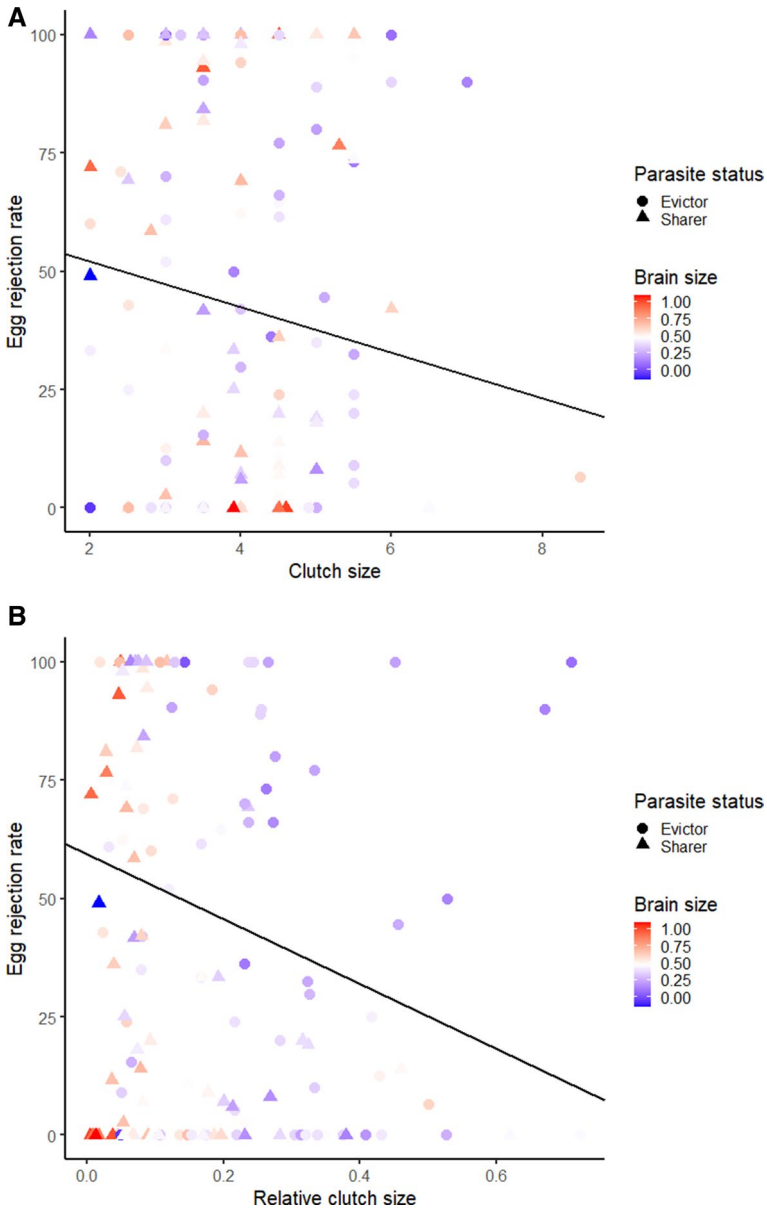


Fig. 1 The negative relationship between absolute clutch size (eggs, x axis: **A**) and relative clutch size (eggs/body mass, x axis: **B**) versus egg rejection rate (%) (y axis) is also impacted negatively by relative brain size (standardized and scaled; dot colors) and show differences between groups of parasite type (dot shapes). The solid black line indicates the intercept and the slope estimated by the corresponding model with phylogenetic controls (see [Results](#)). Note that for these plots we did not use scaled clutch size data

Discussion

The maternal investment hypothesis (*sensu* Hauber et al. 2020) predicts that bird species that lay larger (costlier) clutches are more likely to reject eggs laid by avian obligate brood parasites. However, the predictions of this hypothesis were not supported by our comparative analyses, which used data from the published literature to examine clutch size and rejection rates across species. Instead, we found statistical support for the opposite pattern: larger absolute and relative clutch sizes were consistently associated with higher levels of acceptance of parasitic eggs. Notably, however, for the absolute clutch size variable, the strength of this conclusion comes not from the statistically significant p-values but instead for the consistency of the negative relationship between clutch size and egg rejection rates across top models and model-averaged outputs, while still leaving a substantial amount of variation unexplained in the data sets (e.g., see Fig. 1A for both of these conclusions). In contrast, our relative metric of clutch size (accounting for the known covariation with body size with clutch (negative) and egg (positive) size across species; Saether 1989), showed not only a consistent but also a statistically significant negative relationship with egg rejection rates for the combined species set when accounting for relative brain size (negative predictor of rejection rate) and parasite type (lower rejection rates by nest-sharing parasites' hosts; Fig. 1B).

Our results are, thus, consistent with the alternative hypothesis that egg rejection is constrained by physiological trade-offs between investment in the host's own clutch and the propensity to reject foreign eggs. Such trade-offs could arise because shared endocrine mechanisms may influence both parental care behaviors and egg rejection responses (for example, prolactin increases incubation behavior but decreases egg rejection rates; Ruiz-Raya et al. 2021), but our comparative analyses here cannot identify specific endocrine pathways or other physiological linkages between clutch size and egg rejection propensity. Critically, however, our results are also consistent with the hypothesis that cognitive constraints influence the relationship between clutch size and egg rejection, since it may simply be easier to detect a dissimilar (foreign) egg in a smaller host clutch (an application of Weber's law; *sensu* Akre and Johnsen 2014; Dixit et al. 2021). Tests of these not mutually exclusive mechanisms will require extensive future comparative and experimental studies across species (Abolins-Abols and Hauber 2018; Ruiz-Raya 2021), although limited effect sizes from small-scale intraspecific variation in clutch size or other maternal investment metrics (e.g., Hauber et al. 2020) might still yield strong interspecific patterns in future large-scale comparative tests.

The results here also replicate previous studies, confirming the consistent role of several predictors of egg rejection likelihood across species, including for example morphology (larger body size), biogeography (more northerly breeding latitude), parasite type (hosts are more likely to reject when parasitic chick is an evictor vs. nest-sharer), and the nervous system (smaller relative brain size; Peer and Sealy 2004; Aviles and Garamszegi 2007; Medina and Langmore 2015; Luro and Hauber 2020). However, several studies have found that even these interspecific patterns do not consistently hold up within individual host species. For example, body size was not correlated with egg rejection in American Robins (Abolins-Abols and Hauber 2020b), brain size was not correlated with egg rejection in Cinereous Tits (*Parus cinereus*, Liu et al. 2020), and more northerly breeding latitudes were associated with reduced rather than increased levels of egg rejection in American Robins (Briskie et al. 1992). These apparent contradictions may imply that physiological mechanisms and their functional linkages with behavior vary across host species, and/or

that egg rejection is less flexible within species than across species. The latter pattern could result if the extent of variation in parental care behaviors and their endocrine mediators is smaller within than across species (making such a pattern difficult to detect statistically) or if interindividual variation in rejection probability is confounded by individual (e.g., Hauber et al. 2006) or social (e.g., Thorogood and Davies 2012) experience within and between populations.

Obligate avian brood parasitism impacts ~17% of known bird species and has affected the evolution of host reproductive strategies, including nest construction (Antonson et al. 2020) and egg morphology (Kilner 2006). Our analysis reveals that across host species, a primary defense against parasitism (egg rejection) is inversely correlated with components of maternal investment (absolute and relative clutch sizes). In order to determine whether these traits are functionally linked by shared endocrine mechanisms or other physiological processes, more intraspecific experiments are needed to fuel and power future comparative analyses (sensu Schwabl et al. 2007).

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s10682-022-10165-w>.

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Authors' contributions MEH conceived the study; MEH, CR, and JN conceptualized the study, MEH and JN sourced the data; JN conducted the analyses; MEH and CR wrote the manuscript with input from JN.

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Availability of data and materials The updated data sets used in this study have been deposited into Figshare.com and are made available publicly at: <https://figshare.com/s/e2fa76fa80382edb5d67>.

Code availability Software application or custom code: We did not use custom software or code for this project.

Declarations

Competing interests The authors have not disclosed any competing interests.

Consent for publication All authors agree to the publication of this article.

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