The costs of avian brood parasitism explain variation in egg rejection behaviour in hosts

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Many bird species can reject foreign eggs from their nests. This behaviour is thought to have evolved in response to brood parasites, birds that lay their eggs in the nest of other species. However, not all hosts of brood parasites evict parasitic eggs. In this study, we collate data from egg rejection experiments on 198 species, and perform comparative analyses to understand the conditions under which egg rejection evolves. We found evidence, we believe for the first time in a large-scale comparative analysis, that (i) non-current host species have rejection rates as high as current hosts, (ii) egg rejection is more likely to evolve when the parasite is relatively large compared with its host and (iii) egg rejection is more likely to evolve when the parasite chick evicts all the host eggs from the nest, such as in cuckoos. Our results suggest that the interactions between brood parasites and their hosts have driven the evolution of egg rejection and that variation in the costs inflicted by parasites is fundamental to explaining why only some host species evolve egg rejection.

1. Introduction

Avian brood parasites lay their eggs in the nest of other species, their hosts, who raise a foreign chick [1]. Brood parasitism is costly to the hosts and has been proposed as the driver of the evolution of defences [1], such as attacking parasites [2] or rejecting their chicks or fledglings [3,4]. One of the most intensively studied defences is egg rejection. To date, egg rejection has been studied in around 200 different bird species [5,6]. Surprisingly, despite the effectiveness of egg rejection as a defence against brood parasitism, not all host species reject foreign eggs [5]. There is still no consensus about which particular traits are associated with the evolution of egg rejection [6–8].

Previous studies suggest that several factors may explain variation in egg rejection behaviour. First, the most obvious variable is whether a species is a suitable and a current host of a brood parasite [6]. Suitability is assessed based on the diet of the host chicks and nesting habits [1]. Second, brood parasites vary in the costs they inflict on host fecundity (termed virulence sensu Kilner [9]). Some parasites such as the common cuckoo (Cuculus canorus) inflict very high costs, because the newly hatched parasite evicts all the host’s eggs from the nest (evicting parasites). Conversely, hosts of non-evicting brood parasites (such as the parasitic cowbirds, Molothrus spp.) may succeed in rearing their own progeny alongside the parasite chick [1]. Third, the costs of parasitism can vary between host species. For instance, small hosts that rear large parasites will possibly suffer higher provisioning costs than host species that are of similar size to their parasites [10]. Similarly, hosts (of evicting parasites) that lay large clutches will possibly carry larger costs if their whole brood is lost than hosts with small clutches, so selection for egg rejection should be stronger in the former. Fourth, nest type may be an important predictor of egg rejection, given that poor visibility inside enclosed nests may constrain a host’s ability to discriminate between eggs [6].
Finally, latitude may also be related to egg rejection. Breeding seasons are shorter at high latitudes, which may reduce opportunities for re-nesting following parasitism and lead to stronger selection for egg rejection [6,11].

Here, we compile data on egg rejection rates from 198 avian species and perform a series of comparative analyses to test which of the variables mentioned above can explain the evolution of egg rejection. By using a much larger dataset and recent, more robust phylogenetic techniques and phylogenies than previous studies [6–8,11], we aimed to arrive at a unified understanding of why egg rejection evolves in birds.

2. Methods

(a) Data collection
We obtained egg rejection data for 198 species from published studies (see electronic supplementary material, table S1). We classified host status of species into one of four categories based on data published in the original sources; suitability was based on dietary requirements or nesting habits: (1) unsuitable hosts (n = 15), (2) suitable hosts but have no known reports of parasitism (non-current hosts hereafter, n = 58), (3) hosts of parasites that do not evict host eggs (n = 62) and (4) hosts of parasites that evict all host eggs (n = 63). For known hosts (categories 3 and 4), we also obtained information on whether it was a rare or common host from the original article. We collected information on average clutch size, host nest type, and parasite and host body size from [12] or [13]. Latitudinal distribution was obtained using the function gbi in the Dismo R package [14] (see the electronic supplementary material).

(b) Phylogenetic analyses
To account for phylogenetic relatedness between species, we ran all analyses in 1000 possible phylogenetic trees obtained from www.birdtree.org [15]. To test which variables were the best predictors of egg rejection we ran phylogenetic regressions using the function PGLS in the R package CAPER [16]; in our models, the response variable was percentage of egg rejection per species, and the predictor variables were host status, clutch size, host nest type and host/parasite body size (details in the electronic supplementary material). We report the β estimate and p for each predictor and the λ for the whole model. We also calculated phylogenetic signal on the rate of egg rejection and on host status by using Pagel’s λ in the PHYTOOLS package in R [17]. Higher (closer to 1) and significant values of λ suggest that the distribution of the traits (or the relationships) are linked with the structure of the phylogeny.

3. Results

Host status and egg rejection had a significant phylogenetic signal (host status λ = 0.81, p < 0.001, egg rejection λ = 0.91, p < 0.001, figure 1a). Across all species, egg rejection was predicted by latitude and host status (table 1 and figure 1b). There were higher rejection rates at higher latitudes, and unsuitable hosts had significantly lower egg rejection rates than all the other groups. Non-current hosts had higher rejection rates than hosts of non-evicting parasites (β = −18.34 ± 0.79, p = 0.019 ± 0.0054) and similar rejection rates to hosts of evicting parasites (β = −3.22 ± 0.73, p = 0.39 ± 0.024). Clutch size and nest type did not have any influence on egg rejection rates (β = −5.49 ± 0.181, p = 0.074 ± 0.011 and β = 2.53 ± 0.79, p = 0.72 ± 0.077, λ = 0.88 ± 0.14). For hosts of non-evicting parasites, all predictor variables were non-significant (p > 0.3). For hosts of evicting parasites, the cost of raising a parasitic chick (parasite mass/host mass) was the only significant predictor of egg rejection (table 1 and figure 2), where hosts that are exploited by relatively larger parasites show higher egg rejection. There were no significant differences in egg rejection between common and rare hosts (β = 4.51 ± 0.47, p = 0.65 ± 0.02).

4. Discussion

The best predictor of egg rejection was host status, supporting the argument that egg rejection has evolved as a defence against brood parasitism [6]. Additionally, we found significant phylogenetic signal in host status and egg rejection, suggesting that
phylogenetic relatedness can predict whether a species is a host and a rejecter. This is not surprising, given that hosts are suitable based on traits like diet or nesting habits, which are very likely to be phylogenetically conserved [18,19].

Interestingly, we found that non-current, but suitable host species presented egg rejection rates (mean = 57.99%) that were similar to those of hosts of evicting parasites (mean = 59.03%), suggesting that non-current, suitable hosts may have been hosts in the past. Rothstein [20] proposed that egg rejection carries insignificant costs and may persist as a relic behaviour for years in the absence of brood parasitism, and this has been supported by empirical studies [21] and is discussed in detail in a recent review [5]. Further, our findings suggest that brood parasites switch to a new host when egg rejection becomes a highly reliable defence in their current host, since rejection rates of 100% were more common in non-current hosts (49% of the species) than hosts (21%). These results provide support for both the single trajectory model of brood parasite–host interactions [20], and Soler’s [5] model of a cumulative increase in the number of species with successful resistance; hosts evolve highly effective egg rejection and retain it, leading to a host switch by the parasite.

Brood parasite species differ in the costs they inflict on their hosts; some parasite chicks kill or evict all host young, whereas others tolerate them [9]. As predicted, egg rejection was more likely in hosts of evicting than in hosts of non-evicting parasites. This suggests that there is weaker selection on hosts of non-evicting parasites for the evolution of defences. However, an alternative explanation is the duration of the brood parasite–host association; cuckoos are a much older lineage (approx. 60 Ma) than cowbirds (approx. 3 Ma) and this may also explain why more of their hosts have evolved egg rejection [22]. Also, cowbird species tend to exploit a wider variety of hosts than other brood parasites, and this may lead to lower parasitism rates of individual host species and thereby diffuse the intensity of the interactions with their hosts [22].

The evolution of egg rejection in hosts of evicting parasites (59.03%) and non-evicting parasites (32.84%) appears to be influenced by different variables. In hosts of evicting parasites, the relative size of the parasite and its host can determine whether a species is a rejecter or not. When the host is very small relative to the parasite, it is more likely to evolve egg rejection. Interestingly, this trend was not found for hosts of non-evicting parasites, which supports the idea that costs are higher for hosts of evicting parasites. Our results also confirm that hosts and parasites are more similar in size in the cowbird–host system than in the cuckoo–host system, as has been noted previously [10]. Additionally, we found that latitude is a good predictor of egg rejection behaviour; species at higher latitudes showed higher egg rejection rates. Latitude is highly correlated with seasonality [12]; thus, the pattern detected suggests that egg rejection is more likely to evolve in highly seasonal environments, where opportunities for re-nesting are more scarce, and the costs of being parasitized may be higher [6]. Clutch size and nest type were not predictors of egg rejection in hosts of evicting or non-evicting parasites.

In conclusion, we found support for the idea that non-current hosts can retain egg rejection, which may be a cost-free behaviour, and that the likelihood of evolving egg rejection is influenced by the costs of parasitism; egg rejection is more likely to evolve if all host offspring are lost as a result of parasitism, if the parasite is large relative to the host, and if opportunities for re-nesting following parasitism are low.

**Data accessibility.** The dataset supporting this article has been uploaded as part of the electronic supplementary material.

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