Persisting coevolution of avian hosts and parasites

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The fate of host defensive behaviour in the absence of selection from brood parasitism is critical to long-term host–parasite coevolution. We investigated whether New World Bohemian waxwings Bombycilla garrulus that are allopatric from brown-headed cowbird Molothrus ater and common cuckoo Cuculus canorus parasitism have retained egg rejection behaviour. We found that egg rejection was expressed by 100 per cent of Bohemian waxwings. Our phylogeny revealed that Bohemian and Japanese waxwings Bombycilla japonica were sister taxa, and this clade was sister to the cedar waxwing Bombycilla cedrorum. In addition, there was support for a split between Old and New World Bohemian waxwings. Our molecular clock estimates suggest that egg rejection may have been retained for 2.8–3.0 Myr since New World Bohemian waxwings inherited it from their common ancestor with the rejecter cedar waxwings. These results support the ‘single trajectory model’ of host–brood parasite coevolution that once hosts evolve defences, they are retained, forcing parasites to become more specialized over time.

Keywords: brood parasitism; coevolution; egg rejection; molecular clock; relaxed selection

1. INTRODUCTION

When selection pressures are relaxed, adaptations may decay because they incur costs [1]. However, when adaptations are expressed only in the presence of specific stimuli, they may have no effect on fitness and such neutral traits may persist for long periods after selection has been relaxed [2,3]. Information on how long adaptations are retained or conversely how quickly adaptations are lost in the absence of benefits is relatively scanty (but see [2,4]). Whether adaptations are lost or retained is significant, because an adaptation that is retained or declines slowly may be present if selection is renewed, and therefore may accelerate an evolutionary response to the selection pressure.

We examined the extent to which a behavioural defence persists in the absence of selection from avian brood parasitism. The interactions between avian brood parasites and their hosts are ideal for determining the fate of adaptations once selection has been relaxed, owing to shifting distributions of hosts and parasites [5,6] or the avoidance of well-defended hosts by parasites [7,8]. Host defences such as rejection of parasite eggs may be lost in the absence of selection if birds reject their oddly coloured eggs [9,10], but are more likely to be retained because these behaviours may never be expressed in circumstances other than parasitism [2,3]. Whether host defences persist in the absence of brood parasitism is critical to long-term avian brood parasite–host coevolution. If defences decline quickly, brood parasites can alternate between well-defended hosts and former hosts that have lost most of their defences, owing to the costs of maintaining them once parasitism has ceased, or follow what has been termed the ‘coevolutionary cycles’ model of host–brood parasite coevolution [3]. By contrast, if defences persist for long periods of time, as in the ‘single trajectory model’, brood parasites will have to evolve adaptations such as egg mimicry for one or a small number of hosts, which will force them to become specialized [3].

Cedar waxwings, Bombycilla cedrorum, are hosts of the parasitic brown-headed cowbird, Molothrus ater in North America and eject most cowbird eggs added to their nests [11,12]. Bohemian waxwings Bombycilla garrulus are closely related to cedar waxwings but breed north of the cowbird’s range, with the exception of some overlap in western Canada [13]. This overlap would have little effect on the Bohemian waxwing gene pool because it is extremely rare in this area [13,14], making the Bohemian waxwing an ideal host for testing the validity of the single trajectory model and the extent to which defences are retained in the absence of selection. Here, we tested whether Bohemian waxwings express egg rejection under conditions of relaxed selection, and therefore probably inherited it from a common ancestor with cedar waxwings. We also estimate how long this defence may have persisted under relaxed selection, using an estimate of clade age based on a molecular clock.

2. MATERIAL AND METHODS

Material and methods can be found in the electronic supplementary material.

3. RESULTS

(a) Experimental parasitism

Bohemian waxwings rejected 100 per cent (n = 9 nests) of cowbird eggs after an average of 1.6 days following parasitism (range 1–4 days). No host eggs were damaged or missing following ejections. We videotaped one nest following experimental parasitism and the bird returned to the nest, peered inside, grasped the egg between its mandibles, and flew away with the egg.

(b) Phylogenies and date estimates

Both Cyt b and ND2 genes, under maximum-parsimony and maximum-likelihood criteria, produced similar
topologies with generally high support for clades representing traditional species (B. cedrorum, B. garrulus, and Bombycilla japonica; figure 1). In all analyses, B. garrulus and B. japonica were sister taxa, and this clade was sister to B. cedrorum. In addition, there was support in all analyses for a split between Old World and New World samples of B. garrulus. Combined gene analysis also produced strong support via both inference methods for the topologies found in single gene analyses. Dates for key nodes in the waxwing tree were highly consistent between the two genes, and these indicate that the radiation (basal split) of bombycillid species began roughly 2.79 (ND2) to 2.96 (Cyt b) Myr ago (table 1). The split between New World and Old World populations of B. garrulus was estimated at 1.1–1.5 Myr ago based on ND2 and Cyt b analyses, respectively.

4. DISCUSSION
Bohemian waxwings rejected 100 per cent of cases of experimental parasitism despite being allopatric from brown-headed cowbirds. The biogeographic history of the Bombycillidae lineage is unclear [16], making it difficult to ascertain the dynamics of egg rejection evolution in waxwings; however, there appear to be at least two equally parsimonious scenarios. Cedar waxwings may have originated in the New World, and this is supported by the observation that their closest relatives are New World silky flycatchers [17]. They split into the Old World Bohemian waxwing after colonizing the Old World, which then split into the Japanese waxwing and the New World Bohemian waxwing after recolonizing North America. The alternative scenario is that Old World Bohemian waxwings colonized North America and split into cedar waxwings; Old World Bohemian waxwings also split from Japanese waxwings; and there was a second colonization of the New World by Old World Bohemian waxwings that resulted in the New World Bohemian waxwings. Accordingly, egg rejection may have evolved in response to cowbird parasitism in the Nearctic or cuckoo parasitism in the Palaearctic. However, there are several factors that indicate that the first scenario of cowbird parasitism was the probable selection pressure. Based on current ecologies and ranges, there is greater overlap between cowbirds and cedar waxwings than cuckoos and the two Old World waxwing species [13,18,19]. There are also no records of parasitism on Old World waxwings by any cuckoo species [20], whereas the cedar waxwing is a regular host of the cowbird [21]. Cowbirds parasitize cedar waxwings despite the waxwing's unsuitable frugivorous diet.

Figures and tables have been included for completeness, but not all are relevant to the main content of the discussion.
diet, because cowbirds are generalist parasites and use many hosts [21]. By contrast, cuckoos are specialists [18] and it is unlikely that they were able to specialize on hosts with such an inappropriate diet. Dating estimates indicate that cedar waxwings and New World Bohemian waxwings split 2.8–3.0 Myr ago, suggesting that egg rejection may have been retained in Bohemian waxwings through speciation for the same length of time in the absence of parasitism. However, an extinct brood parasite species may have parasitized Bohemian waxwings in the past. Cowbirds may also have been more widespread at the end of the Pleistocene [22] and Bohemian waxwings may have been parasitized during this time. If true, rejection still has been retained at fixation in this species for at least 8000–10 000 years. Regardless, these data clearly indicate that host defences such as egg rejection can be retained for long periods of time in the absence of selection.

Cedar waxwings reject 69 per cent of cowbird eggs (n = 58 nests) and are unique among cowbird hosts in that they reject eggs at a higher frequency during the laying period of the nesting cycle (87.5%) compared with the incubation stage (40%) [12]. Bohemian waxwings rejected eggs regardless of when they were added to nests. Cedar waxwings damage their eggs when attempting to puncture-eject cowbird eggs because of smaller bills, but the Bohemian waxwing we observed grasp-ejected the artificial egg and removed it.

Only four selection pressures are known to favour egg rejection [23] and the only one, other than interspecific parasitism, that could account for rejection in passerines such as Bohemian waxwings is conspecific brood parasitism. However, conspecific parasitism rarely selects for rejection because of the similarity between the eggs of conspecifics, and this form of parasitism has never been reported in Bohemian waxwings or the better studied cedar waxwing [13,19].

Our findings and others [2,3,5,23,24] (but see [10]) suggest that anti-parasite behaviours persist in many hosts in the absence of parasitism for long periods of time and support the single trajectory model of host–avian brood parasite coevolution in which whole host communities become increasingly resistant to brood parasitism. As more hosts evolve and retain defences, parasites are forced to circumvent them through the evolution of egg mimicry; however, because host species have eggs that differ, parasites will only be able to mimic one or a small number of hosts. Anti-brood parasite behaviours are yet another of an increasing number of examples of long-term retention of behaviours after the relaxation of selection pressures [1] that have potential consequences on present day behaviour.

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