Research

Inter-specific brood parasitism and the evolution of avian reproductive strategies

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Avian brood parasitism is a potent selective agent modulating host behaviors and morphology, although its role in determining diversification of avian breeding strategies remains elusive. Hitherto, the study of selection of brood parasites on host breeding strategies has been based on single reproductive trait approaches, which neglect that evolutionary responses to brood parasites may involve co-ordinated changes in several aspects of reproduction. Here I consider covariation among reproductive traits to test whether parental breeding strategies of hosts of brown headed cowbird (BHC hereafter) in North America and the common cuckoo (CC hereafter) in Europe, two parasites with contrasting level of virulence, have evolved in response to brood parasitism. The effect of parasitism on avian breeding strategies differed between continents. Long term exposure to BHC parasitism selected for a lower breeding investment in North America, but not so CC parasitism in Europe. These results suggest a key role of parasite virulence on the evolution of avian breeding strategies and that brood parasitism has selected for a co-ordinated breeding strategy of reducing parasitism costs by shortening and fractioning reproductive events within a single season in North America.

Keywords: birds, brood parasitism, breeding strategies, life-history evolution

Introduction

About one per cent of extant birds are obligate brood parasites, that is to say they lay their eggs in the nests of another species (i.e. the host), which carries out the parental duties, from the incubation of eggs to chick feeding (Rothstein 1990, Davies 2000). Raising a non-related brood parasite often inflict severe fecundity costs to hosts (Payne 1977, Rothstein 1990), and has resulted in the evolution of behavioral defenses, such as mobbing of parasites (Røskaft et al. 2002, Welbergen and Davies 2009), and rejection of parasite eggs (Davies and Brooke 1988, Soler and Møller 1990, Moksnes et al. 1991, Avilés et al. 2010, Spottiswoode and Stevens 2010) and nestlings (Langmore et al. 2003, Grim 2007, Sato et al. 2010, Tokue and Ueda 2010). Brood parasites have also selected for morphological changes in hosts, such as changes in

egg appearance (Davies and Brooke 1989, Avilés and Møller 2003, Stokke et al. 2002) and nestling color designs (Hauber and Kilner 2007).

Evolutionary responses to brood parasitism may be also evident in aspects of host breeding strategy (Svensson and Råberg 2010, Medina and Langmore 2016, Avilés 2018). Models of life-history evolution predict a decrease of parental breeding effort whenever juvenile survival is reduced, which is typically the case for hosts of avian brood parasites (Hauber 2003, Servedio and Hauber 2006). Tests of this expectation have mostly targeted on reporting a negative association between intensity of brood parasitism and avian clutch size, as a trait likely reflecting avian breeding effort. In agreement, a comparative study has shown that host species with long-term exposure to brown-headed cowbird *Molothrus ater* (BHC hereafter) parasitism have lower clutch sizes than new hosts (Hauber 2003). However, that study was based on a reduced number of species (non-hosts were excluded), and, did not control for differences in latitude known to affect breeding traits (Jetz et al. 2008). Moreover, different avian brood parasite species may select for different host reproductive strategies, as they differ in virulence (Kilner 2005). Indeed, a recent comparative study has shown that hosts of inter-specific brood parasites in Australia, Africa and Europe do not have smaller clutches, but that hosts that incur large costs from raising a parasite lay larger clutches (Medina et al. 2017). Medina et al. (2017) modeled the evolution of clutch size in relation to parasitism and concluded that an increase in clutch size (or no change) would be the most likely evolutionary outcome if it is considered that any breeding attempt, including those produced by one host individual after having experience parasitism, might be parasitized. Hence in the light of contrasting results and predictions from theoretical models, it remains debatable if avian brood parasitism has selected for one or more reproductive tactics in their hosts.

A major difficulty for the understanding of the role of brood parasites in determining the diversification of avian breeding strategies is that previous studies considered the mean value of a single reproductive trait as dependent variable in models assessing the effect of parasitism (Soler et al. 2001, Hauber 2003, Remeš 2006, Medina et al. 2017). This univariate approach is misleading, as it ignores the fact that different features of the breeding strategy are likely inter-related through the energetic tradeoffs between number and size of offspring and current and future reproduction (Roff 2002, Stearns 1992) and hence may contribute to host reproductive success in an integrated way (Bennett and Owens 2002, Lack 1968). For instance, there is compelling evidence of a tradeoff between egg volume and clutch size in birds (Martin 1987, Blackburn 1991, Potti 1993), and previous comparative evidence provides support for the view that clutch size might be a byproduct of annual productivity and number of brood attempts (Martin and Li 1992). Hence, in those brood parasite systems where the parasite nestling is grown together with host offspring, parasitism may exert selection on host egg size as larger eggs will produce more competitive nestlings

(Krist 2011). The facts that different aspects of reproduction may contribute to produce an adaptive response, and that they covary, require that evolutionary responses to brood parasites involved co-ordinated changes in all aspect of reproduction (Bennett and Owens 2002).

The main aim of this study is to consider potential functional linkages between different aspects of avian reproduction in order to understand how selection by the common cuckoo (CC hereafter) *Cuculus canorus* and BHC parasitism has shaped the evolution of avian breeding strategies. BHC and CC parasitism represent the two extremes of a gradient of parasite virulence (i.e. BHC are frequently raised together with host nestlings, whereas in Europe the CC hatchling evicts out of the nest the host eggs, rendering the complete loss of the host reproduction, Kilner 2005). Theoretical models have stressed that changes in the breeding strategy to buffer the costs of brood parasitism (i.e. tolerance defences sensu Svensson and Råberg 2010) will be favoured in hosts of the less virulent brood parasites (Medina and Langmore 2016). This is so because in these species fecundity costs due to rejection errors (i.e. erroneous rejection of the host's own eggs and costs due to accidental breakage of the host's own eggs during egg rejection (sensu Lotem et al. 1995)) will be particularly high because hosts would lose the chance of raising one or more of their own eggs, which might be possible if the nest is parasitized (Stokke et al. 2005, Medina and Langmore 2016). I thus predict 1) that intensity of parasitism is associated with avian breeding strategies in North America but not in Europe. Regarding the direction of the effect of parasitism on breeding strategies, it can be predicted 2) that long term exposure to brood parasitism selected for a co-ordinated breeding strategy of reducing parasitism costs by shortening and fractioning host reproductive events within a single season in North America, but not in Europe.

Methods

Sampled species

I gathered complete information on breeding traits and level of brood parasitism for 276 species (144 European and 132 North American species, respectively, Supplementary material Appendix 1 Table A1). I specifically deal with hosts of the BHC and the CC in the Northern Hemisphere for two mean reasons. First, there is much available information that allows reconstruction of the interaction history between brood-parasites and hosts in North America and Europe; and, second, the BHC and the CC are the only widely distributed multi-specific brood parasites in North America and in Europe, so that adaptations in the breeding strategy in response to brood parasites other than the BHC and the CC are unlikely. I specifically disregarded brood parasites in Africa and Australasia because in these regions several brood parasitic species coexist over large distributional areas, and, because these may currently parasitize or may have parasitized in the past the same

host, hence impeding a neat tracking of continental changes in the host breeding strategy in relation to parasites.

Breeding traits

I collated average value per species on egg volume, clutch size, length of the nestling period and number of breeding attempts per season from different sources (Harrison 1975, Cramp 1998, Del Hoyo et al. 2007, Baicich and Harrison 2005).

Level of parasitism

I classified species regarding parasitism level using three categories reflecting increased levels of brood parasitism. North American species were primarily categorized as either hosts or non-hosts of the brown-headed cowbird based on Friedmann et al. (1977). Forest species that were not mentioned in Friedmann et al. (1977) were considered as non-hosts (see also Soler 2014). Cowbirds have expanded their breeding range in North America (Mayfield 1965, Rothstein 1994). As a consequence they have penetrated into the forest of North America, and have come in contact with new hosts (woodland species) with no previous history of contact with a brood parasite. Therefore, I distinguished between old and new hosts based on breeding habitat, as this relates to the level of long-term exposure to cowbird parasitism (Hosoi and Rothstein 2000, Remeš 2006). Host species breeding into forests were categorized as new hosts, and host species breeding in the edge, shrub, marshes and open lands were classified as old hosts (Supplementary material Appendix 1 Table A1). For European species, those reported as frequently parasitized by the common cuckoo in Wyllie (1981) were considered as old hosts. Species not reported as frequently parasitized by Wyllie (1981) but that Moksnes and Røskaft (1995) reported to be parasitized by the common cuckoo at least 25 times were considered in an intermediate category (new host). All other species were considered non-hosts (Supplementary material Appendix 1 Table A1). I assume throughout the paper that 'new hosts' category reflects a biologically meaningful intermediate state in the transition from non-parasitism to long-term exposure to brood parasitism.

It can be argued that current parasitism categorized according to the number records may not reliably reflect past parasitism in Europe and hence true selection of brood parasites on breeding traits. To validate this assumption I further classified European species for their long-term suitability to raise a brood parasite based on basic aspects of their biology (Davies and Brooke 1989, Moksnes and Røskaft 1995, Stokke et al. 2002, Garamszegi and Avilés 2005). Suitable hosts have more likely experienced a long-term interaction with brood parasites than unsuitable ones, thus potentially providing better chances for selection on breeding traits. I classified species in relation to suitability as a host based on information collated from the Handbook of the Birds of the World (Del Hoyo et al. 2007), and the complete birds of the western Palearctic (Cramp 1998). Species were coded as

unsuitable brood parasite hosts (score of 0) either because: 1) they are hole-nesting birds or build their nests in concealed places which makes egg laying difficult for the parasite, 2) because they feed their chicks with food unsuitable for the parasite chick (mainly seed eaters), 3) or because they have eggs or chicks very dissimilar in size with those of the parasite. A fraction of species can be regarded either as suitable or unsuitable hosts, since in some parts of their range they are available as hosts, but not in other parts, or because they inhabit treeless areas where perching is not possible for the brood parasite. I included these species in an intermediate group of partially suitable hosts (score of 1). The rest of the species were coded as suitable hosts (score of 2) (Supplementary material Appendix 1 Table A1). A PGLS revealed that level of parasitism in Europe was positively related with long-term suitability to raise a brood parasite (Supplementary material Appendix 1 Fig. A1), suggesting that that current levels of parasitism based on number of records reliably reflect the extent of selection on breeding traits in Europe. Nonetheless, to be on the safe side, I also report phylogenetic corrected pair-wise comparisons in which the 'new host' category was excluded, thus allowing a more neat comparison between non-host and old hosts.

Confounds

To control for a possible effect of body size on avian breeding strategies, I obtained body-mass information for each species from Dunning (1992) and log10 transformed it prior to analysis. Differences in research effort may result in biases in detection of brood parasitism in different species, as parasitism will be more likely reported in more intensely studied species (Garamszegi and Avilés 2005). Hence I estimated research effort for each species based on number of published article since 1972, as cited in the ISI Web of Science and included this predictor as a variable in models including parasitism. In addition, previous comparative work has shown that avian breeding traits change with latitude (Jetz et al. 2008). Therefore, to control for a potential effect of latitude, I calculated latitude midpoint between the most northern and southern breeding location based on distributional maps of species reported in IUCN Red List for birds (BirdLife International 2018). Finally, it has been previously shown that avian life-history traits vary with nesting site because of differences in nest predation rates (Martin and Li 1992). Thus I classified species as either open nester (score of zero) or hole nester (score of 1, including domed and cavity nesters) based on Harrison (Harrison 1975, Baicich and Harrison 2005).

Phylogeny

Species cannot be considered statistically independent observations, and a phylogenetic control is required to eliminate the confounding effects of common ancestry (Felsenstein 1985). To control for phylogenetic relatedness in the analyses I downloaded 100 randomly extracted phylogenetic trees

including all the considered species from the most recent comprehensive time-calibrated set of complete phylogenies of extant bird species (<<http://birdtree.org>>, Jetz et al. 2012). I subsequently tested for the effect of phylogenetic uncertainty by repeating every model with each of these 100 random phylogenies.

Data analyses

To combine breeding traits I conducted phylogenetic principal component analyses (PPCA, Revell 2009) based on the 276 species using the R package 'phytools' (Revell 2012). The species scores of the PPCA were then used to define the position of each species regarding the combination of breeding traits that best defined the breeding strategy. I performed phylogenetic generalized least squares regressions (PGLS) using the R packages 'nlme' (Pinheiro et al. 2011) and 'ape' (Paradis et al. 2004) to study the relationship between scores of the PPCA and parasitism. Scores of the PPCA on host breeding traits were used as dependent variables in two multiple predictor models, containing body mass, nest type, parasitism, research effort, and latitude as predictors. Because the effect of brood parasitism on breeding strategies is expected to vary between European and North-American, I also fitted continent, and, the interaction between continent and parasitism, as explanatory terms to these models. From the maximal models I built a set of candidate models involving different combinations of predictors, and determined the best-fit models using Akaike's information criterion with the correction for small sample sizes (known as AICc) (Burnham and Anderson 2002) (Supplementary material Appendix 1 Table A2). All candidate phylogenetic models included body mass as a predictor and were run on a majority-rule consensus tree calculated on the 100 random phylogenies. I have also included in the appendix a similar set of phylogenetic analyses based on clutch size as the dependent variable allowing a direct comparison with previous studies testing the effect of brood parasitism on clutch size (Hauber 2003, Medina et al. 2017). There is huge variation in sample sizes for the different categories between Europe and North America (Supplementary material Appendix 1 Table A1, Fig. A2). Hence, after identifying the best-fit models, pairwise comparisons were used to check for robustness of results.

Prior to running PGLS models, I assessed collinearity by examining the VIF values of the explanatory variables, all of which were always lower than 3 (Zuur 2009).

Aiming to deal with sensitivity of the model estimates to the phylogenetic hypothesis, I reassessed all the relationships between traits in best fitting models using ML on the set of 100 randomly selected phylogenetic trees using the R package AICcmodavg (Mazerolle 2011). Parameter estimates were obtained from the resulting models, which allowed calculating average effects and 95% confidence limits from the variance of model parameters across models associated with different trees. This confidence limit interval can thus be interpreted as a consequence of the uncertainty in the phylogenetic hypothesis (see details in Garamszegi and Mundry

2014), and therefore if zero is not contained within its limits provides strong support that $\beta \neq 0$.

The fit of each PGLS to the data was improved by estimating and fitting the maximum likelihood value of Pagel's λ (Freckleton et al. 2002). Body mass and research effort were log-transformed prior to analyses; all other variables were used untransformed.

Results

Variation in avian breeding traits

The phylogenetic principal component analyses showed huge variation in avian breeding traits among species (Fig. 1). Together the two first components explained 64.8% of the total variance in breeding traits, and all breeding variables had high loading values on these two first components (Table 1). Measures of egg volume and length of the nestling period loaded positively on the first principal component (pPC1, Table 1). Clutch size loaded negatively on the second principal component, whereas probability of multiple nesting loaded positively (pPC2, Table 1). Therefore pPC1 separated species into those with large egg volume and long duration of their nestling period and those with small egg volume and short duration of their nestling period. On the other hand pPC2 separated species into those with multiple nesting attempts and small clutch size on one side, and those with a single nesting attempt and large clutch size on the other side.

Breeding traits and brood parasitism

Avian breeding traits were influenced by brood parasitism. Neither of the two best candidate models (i.e. $\Delta AICc < 2$) included parasitism as a significant predictor of pPC1 scores (Supplementary material Appendix 1 Table A2, Table 2). However, pPC2 scores did significantly associate with parasitism level in interaction with continent in the best candidate model (Supplementary material Appendix 1 Table A2), and model averaged estimates accounting for phylogenetic uncertainty corroborated the significance of this interaction (Table 2): the trend to have multiple nesting attempts per breeding season combined with a reduced clutch size characterizing a shortening and fractioning breeding strategy increased with parasitism level in North America, but not in Europe (Fig. 2). Raw analyses based on clutch size qualitatively confirmed patterns based on pPC2 scores (Supplementary material Appendix 1 Table A3–A4, Fig. A2).

Pair-wise comparisons revealed that old hosts of the brown headed cowbird in North America had significantly higher pPC2 scores than old hosts of the common cuckoo in Europe (PGLS, β (lower CL, higher CL) for continent = 6.60 (3.82, 9.38), Fig. 2). Contrary to expectation, however, non-host species in North America showed significantly higher pPC2 scores than non-host species in Europe (PGLS, β (lower CL, higher CL) for continent = 3.30 (1.53, 5.17), Fig. 2). Old and non hosts did not differ in pPC2 scores in Europe (PGLS,

Figure 1. Random possible phylogeny of species included in this study (n=276 species). Branch colors indicate reconstructed ancestral states for breeding traits (pPC1 (A) and pPC2 (B)). Colors at the tip of the tree represent current states of breeding traits (i.e. pPC scores) and grey bars represent information on levels of parasitism for each studied species. Bar length represents variation in levels of parasitism, with the longest bars corresponding with heavily parasitized and the shortest ones with non-parasitized host species, respectively.

β (lower CL, higher CL) for parasitism = 0.74 (−0.85, 2.33), Fig. 2), but old hosts had significantly higher pPC2 scores than non-hosts in North America (PGLS, β (lower CL,

Table 1. Phylogenetic principal component analysis for avian breeding traits (n=276 species). Factor loadings larger than 0.50 are shown in bold.

$\lambda=0.96$				
Phylogenetic PCA				
Standard deviations				
	pPC1	pPC2	pPC3	pPC4
	1.18	1.09	0.91	0.76
Factor loadings				
	pPC1	pPC2	pPC3	pPC4
egg volume	0.83	−0.11	0.17	0.52
clutch size	−0.41	−0.70	−0.50	0.31
duration of nesting period	0.74	−0.23	−0.49	−0.40
multiple nesting	−0.03	0.80	−0.55	0.23
% of variance	35.10	29.77	20.58	14.55

higher CL) for parasitism = 3.20 (1.21, 5.18), Fig. 2), suggesting that the above reported interaction between continent and parasitism was not due to the difference in sample size for the ‘new hosts’ category between Europe and North America (Fig. 2).

The effect of brood parasitism on avian breeding traits was independent of the effect of nest type, latitude and body mass (Table 2): open-nesting species had lower pPC1 scores (i.e. small egg volume and short duration of their nestling period) and higher pPC2 scores than hole-nester species (Supplementary material Appendix 1 Fig. A3); species breeding at northern latitudes had lower pPC1 and pPC2 scores than those breeding at southern latitudes (Supplementary material Appendix 1 Fig. A3), and larger species had higher pPC1 scores relative to small ones (Table 2).

Discussion

Brood parasitism and avian breeding strategies

The influence of brood parasitism on avian breeding traits varied between continents when covariation among different components of the breeding strategy and phylogeny were simultaneously considered. As expected (prediction 1), increased levels of BHC parasitism were associated with a trend to have multiple nesting attempts per breeding season combined with a reduced clutch size in North America. In Europe, however, increased levels of CC parasitism did not relate to avian breeding traits, suggesting that CC parasitism may have played a negligible role on the evolution of the breeding strategy of the European avifauna. An alternative interpretation would be that some of the ‘non-hosts’ in Europe were actually ‘no longer used’ hosts gaining the arms race with the CC, which would suggest that the pattern is difficult to interpret in terms of long-term exposure to CC in Europe. However, this seems unlikely because current levels of parasitism reliably reflect long-term suitability to raise a brood parasite in Europe.

Continental differences in the effect of brood parasitism on avian breeding traits can be explained by differences in virulence between BHC and CC (Medina and Langmore

Table 2. Phylogenetic generalized least-square models testing for the effect of brood parasitism on avian breeding traits (i.e. pPC1 and pPC2 scores derived from a pPCA on host breeding traits) in top models selected by multimodel inference. To deal with phylogenetic uncertainty model average values of estimates and 95% CL are based on PGLS models with 100 different phylogenetic trees. Bold type is used to remark support for $\beta \neq 0$.

	β (SE) ^a	Lower CL	Higher CL
Dependent variable: pPC1 scores (276 species)			
Model 1: pPC1~ Body mass+ Nest type+ Latitude			
Intercept	-30.49 (3.72)	-37.78	-23.20
Body mass	20.36 (1.01)	18.38	22.35
Nest type	1.69 (0.64)	0.44	2.93
Latitude	-0.03 (0.02)	-0.07	-0.004
Model 2: pPC1~ Body mass+ Nest type+ Latitude+ Continent			
Intercept	-29.99 (3.78)	-37.40	-22.58
Body mass	20.31 (1.01)	18.33	22.90
Nest type	1.66 (0.64)	0.42	2.92
Latitude	-0.04 (0.02)	-0.07	-0.007
Continent	-0.42 (0.61)	-1.61	0.77
Dependent variable: pPC2 scores (276 species)			
Model 1: pPC2~ Body mass+ Nest type+ Latitude+ Continent+ Parasitism+ Research effort+ Continent $\times$ Parasitism			
Intercept	6.69 (4.30)	-1.75	15.13
Body mass	-2.26 (1.23)	-4.67	0.15
Nest type	-2.20 (0.79)	-3.77	-0.63
Latitude	-0.07 (0.02)	-0.12	-0.02
Continent	1.42 (1.16)	-0.85	3.69
Parasitism	0.16 (0.39)	-0.60	0.93
Research effort	-0.09 (0.42)	-0.93	0.73
Continent $\times$ Parasitism	1.32 (0.57)	0.22	2.43

^a SE include both sampling error and phylogenetic variance across the set of 100 randomly selected phylogenies used to test the association.

2016). Given that the CC is highly virulent and destroys all the breeding outcome of its hosts (Kilner 2005), there would be no chance for hosts to adjust their breeding traits to minimize the costs of parasitism. Therefore, resistance defenses such as egg rejection, which operates to avoid parasitism at earlier stages of the host reproductive cycle (Svensson and Råberg 2010), should more likely be selected. By contrast, in hosts of the less virulent BHC, fecundity costs associated with the expression of resistance due to rejection errors might be particularly high because hosts may lose the chance of raising one or more of their eggs, which may still survive if the nest is parasitized (Kilner 2005). Supporting this argument egg rejection is more common among hosts of highly virulent brood parasites than among hosts of less virulent ones (Medina and Langmore 2016).

Previous comparative and theoretical studies have long explained low levels of resistance against BHC compared to those of hosts of the CC in terms of the evolutionary lag hypothesis (Rothstein 1990, Davies 2000). Given that the BHC has only recently expanded its distribution in North America, they may have encountered new suitable host populations and species, that would have not had time to evolve recognition and rejection of BHC eggs (Hosoi and Rothstein 2000). An alternative possibility based on my findings would be that differences in virulence between

the BHC and the CC may have favored the evolution of a different kind of defense (i.e. resistance versus tolerance) in North America and Europe. If BHC host adjustments in breeding traits can somehow mitigate the costs of brood parasites (i.e. tolerance defences sensu Svensson and Råberg 2010, Medina and Langmore 2016) selection for resistance mechanisms (i.e. rejection of parasite eggs) should be lower in North America than in Europe. Further insights about this possibility can be obtained by looking at the relationship between rejection behavior and reproductive traits of BHC hosts.

There is at least one alternative possibility for the pattern of covariation between breeding traits and parasitism in North America. Avian brood parasites may select among hosts based on variation in their breeding traits, which informs on parental qualities for parasite offspring (Parejo and Avilés 2007). Accordingly, cowbird females may have selected host species based on particular breeding attributes because these signal a better provisioning of nestlings, giving rise to the association I found between parasitism and pPC2 scores (Fig. 2). Comparative evidence has reported the existence of a trade-off between fecundity and parental care in birds (Badyaev and Ghalambor 2001); hence cowbirds may parasitize species with low fecundity in terms of receiving more food. However, parasite selection based on breeding traits seems

Figure 2. Boxplot showing avian breeding traits in relationship to parasitism in Europe and North America. pPC2 scores are derived from the phylogenetic principal component analysis on four breeding traits (Table 1). High positive pPC2 scores identify species with multiple nesting attempts and a small clutch size. To account for phylogenetic non-independence and potential confounding effects relative pPC2 scores are calculated as the residuals of the PGLS model between the pPC2 scores and log-transformed body mass, latitude and nest type (Table 2).

unlikely because BHC females mostly lay their eggs before hosts have completed their clutches (Friedmann 1929) and hence would have no chance for eavesdropping on complete clutches. Moreover, recent experimental work would suggest that female cowbirds make decisions about which hosts to use based on information of past cowbird breeding success rather than cueing on host breeding success (Louder et al. 2015), which would suggest a minor role of selection based on host breeding traits. Finally, parasite selection does not explain the absence of a relationship between CC parasitism and pPC2scores in Europe.

The reported association between intensity of parasitism and proneness to a shortening and fractioning of the breeding strategy in North America is in agreement with expectation from life-history theory models predicting a decrease in parental effort whenever juvenile survival is affected by brood parasitism (Hauber 2003, Servedio and Hauber 2006, prediction 2). Previous comparative findings on a reduced sample of BHC hosts had shown a negative relationship between clutch size and parasitism (Hauber 2003), although did not account for covariation with other components of the breeding strategy, and for the effect of latitude in the analyses. Hence, the association reported here between pPC2

scores and parasitism intensity constitutes the first comparative evidence that avian brood parasites may have driven the evolution of avian reproductive strategies, at least in North America. Species that have been largely exposed to BHC parasitism follow a tradeoff strategy consisting in reducing their clutch size and increasing the number of breeding attempts. Parasitized hosts with reduced clutches will lose less fitness only if they have chance of having a second unparasitized breeding attempt in the same season (Medina et al. 2017). Currently there is some evidence showing that risk of BHC parasitism of a second host breeding attempt is lower than that of a first breeding attempt (Hauber 2001, Hoover et al. 2006).

My findings on BHC hosts contrast with what was found for highly virulent parasites by Medina et al. (2017), who found a positive relationship between clutch size and the cost of raising a brood parasite. In that study, Medina et al. (2017) did not directly measure the strength of selection by brood parasites, but derived it from differences in size between hosts and parasites, and, therefore an allometric effect on clutch size cannot be excluded. New analyses based on true rather than on size-estimated costs of brood parasites are needed to clarify this issue.

Continental differences in avian breeding strategies cannot be solely explained by the effect of brood parasitism. Indeed pair-wise comparisons between non-host species reveals that American species have more proneness to have multiple nesting attempts and reduced clutch size (i.e. high pPC2 scores) compared with European species. There is previous comparative evidence showing that avian nest predation is lower in Europe than in North America (Martin and Clobert 1996), which may explain the higher fecundity (i.e. larger clutch sizes) and reduced iteroparity (i.e. lower number of breeding attempts per season) of European species as compared to North American ones reported here. Moreover, the role of predation can also be inferred by the found relationship between nest type and breeding traits (Supplementary material Appendix 1 Fig. A2). Hole-nesting birds experience lower nest predation rates than open nesting bird species (Martin 1995), which would fit with the found pattern of lower fecundity and increased iteroparity detected among open-nester species. Alternatively, differences between non-host species among continents might be driven by differences in habitat use as all non-hosts are forest species in North America, whereas in Europe many non-host species of the cuckoo are non-forest species.

Conclusions

These results support the idea that avian brood parasitism might be a potent selective agent acting on breeding strategies of birds in North America but not in Europe, which may point toward a fundamental role of parasite virulence on the evolution of avian breeding strategies. In addition, these results agree with expectation from life-history theory models predicting a decrease in parental effort whenever juvenile survival is affected by brood parasitism.

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Supplementary material (available online as Appendix oik-05686 at <www.oikosjournal.org/appendix/oik-05686>).
Appendix 1.